Dissertationes Forestales 305

Vegetation, nutrients, and CO_2 flux dynamics in northern boreal forests

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Academic dissertation

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ABSTRACT

The growing conditions in northern boreal forests have remained similar for millennia. However, amplified climate change may cause higher mean annual temperatures and precipitation sums, longer growing seasons, along with increased occurrence of extreme weather events (drought, heavy rain, or summertime frost) in the region. The relationship that forest vegetation has with soil nutrients and the exchange of carbon dioxide (CO_2) between the forest and atmosphere may change. This dissertation focuses on quantifying the baseline status of northern boreal forests from these aspects, to be able to predict the upcoming changes more precisely. Soil total phosphorus (P) and nitrogen (N) contents were important factors in explaining the community composition of understory vegetation in the study site. The site was located in a region near a phosphate ore, where soil nutrient contents are highly variable. The number of herb, grass, and sedge species increased with N and P contents in the humus, especially with P. The increasing P content, on the other hand, positively correlated with downy birch (*Betula pubescens* Ehrh.), which was the dominant tree species of the research plot.

The understory vegetation had an important role in the CO_2 exchange rates of a northern boreal Scots pine (*Pinus sylvestris* L.) forest site. The annual CO_2 dynamics varied between the canopy and understory, so that when the canopy began photosynthesizing in the spring, the understory was still under snow cover. The cumulative temperature sum had a higher positive correlation with photosynthesis than the total ecosystem respiration (TER) rate of the pine site. Overall, the pine site was a weak carbon sink during the growing season, although it temporarily turned into a carbon source during a cold and rainy summer.

Extreme weather events, and their effects on the CO_2 dynamics of forests, were studied on a Scots pine site and a Norway spruce (*Picea abies* (L.) Karst.) site. Both sites had experienced extreme summers during the studied times, but the CO_2 flux rates in the Norway spruce site responded more clearly to them. The TER rates of the Norway spruce forest declined when it was warm and dry. This likely happened because of decreased decomposition of organic matter. The decline was, however, only temporary, and TER returned to normal when the temperature and precipitation returned to their average levels. Thus, the studied forest sites seemed to, so far, be rather resilient towards extreme weather events.

Several studies have found that N availability will increase because of warmer temperatures, which speeds up decomposition and nutrient mineralization. However, decomposition may potentially slow down in some spruce forests due to heat. Local variation may thus be high when it comes to the availability of nutrients or to the CO_2 dynamics of forests. While modeling studies are important for predicting the responses of northern forests to climate change on the large scale, our research reminds that local-scale studies are also inevitable for gaining a more precise picture.

Keywords: climate change, carbon, nitrogen, phosphorus, atmosphere, extreme events, northern boreal

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Never had I imagined that I would write the summary part of this dissertation in our kitchen during a time of social distancing caused by a pandemic. Yet, there I was, spending half the day intensively writing and half the day doing whatever it was that interested a three-year-old the most at that time. It is safe to say that the spring was a whirl of emotions from pure joy to frustration in all aspects of life.

Despite writing the summary in almost solitude, I would not have gotten this far without other people. I have been lucky to have two supervisors, who have encouraged and supported in good times, and when things have not gone as planned. I thank my main supervisor Prof. Jaana Bäck for trusting that I can do my work whether it is fieldwork in Lapland or writing in Helsinki. Every time I have had some issues with work, things have started to feel easier after talking to you. There was also a time when my motivation towards my own research was gone. You found me something else to do for a couple of months, and that was exactly what I needed. Dr. Liisa Kulmala has not been an official supervisor for very long, but has surely supervised my work for at least a couple of years when working on articles together. I admire your energy and positivity. You have the skills to give constructive feedback so that it does not let the other person down. I highly appreciate that as a young scientist who does not yet have much experience from writing scientific articles. My other co-authors have also been very helpful and patient. Special thanks to Dr. Maija Salemaa for persistently helping me with the first article and its analyses. Thank you senior lecturer Maj-Lena Linderson for accepting our invitation to act as my opponent. I also want to thank Prof. Eva-Stiina Tuittila and Assoc. prof. Matthias Peichl, who took time and carefully pre-examined this dissertation, and Stella Thompson, who corrected the grammar of the summary.

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Helsinki November 2020,
Laura Matkala

LIST OF ORIGINAL ARTICLES

This dissertation is based on the following four articles, which are referred to in the text by their Roman numerals. All papers are reproduced with the permission of the publisher.

I. **Matkala, L.**, Salemaa, M., & Bäck, J. (2020). Soil total phosphorus and nitrogen explain vegetation community composition in a northern forest ecosystem near a phosphate massif. Biogeosciences 17(6): 1535-1556. https://doi.org/10.5194/bg-17-1535-2020

II. Kulmala, L., Pumpanen, J., Kolari, P., Dengel, S., Berninger, F., Köster, K., **Matkala, L.**, Vanhatalo, A., Vesala, T., & Bäck, J. (2019). Inter- and intra-annual dynamics of photosynthesis differ between forest floor vegetation and tree canopy in a subarctic Scots pine stand. Agricultural and Forest Meteorology 271: 1-11. https://doi.org/10.1016/j.agrformet.2019.02.029

III. **Matkala, L.**, Kulmala, L., Kolari, P., Aurela, M., & Bäck, J. (2020). Resilience of subarctic Scots pine and Norway spruce forests to extreme weather events. Agricultural and Forest Meteorology (in press) https://doi.org/10.1016/j.agrformet.2020.108239

AUTHOR CONTRIBUTION

Laura Matkala (LM) was responsible for the summary of this thesis. In article **I**, LM was responsible for planning the study set up, conducted all fieldwork, laboratory and statistical analyses, and led the writing process. In article **II**, Liisa Kulmala was the corresponding author, LM was responsible for the practical planning of the biomass and growth increment measurements, and for conducting the measurements and analyzing the raw data, as well as served as a co-author of the article. In article **III**, LM was responsible for the data analyses, statistical analyses, and for leading the writing process.

TABLE OF CONTENTS

1. INTRODUCTION

1.1 Special features of northern boreal forests and potential future changes

The northern boreal subzone is located in the uppermost part of the boreal zone (Hämet-Ahti 1981). There, the subarctic climate shapes vegetation with cold temperatures and short growing seasons, which last approximately four months. The biological processes, such as growth or the decomposition of organic matter, and the following release of nutrients are slow (Hobbie et al. 2002). Unlike in the Arctic, where conditions do not allow tree regeneration, the northern boreal zone has forests. Typical northern boreal forests have lower precipitation rates than the more southern boreal subzones (Hämet-Ahti 1981), yet because of cold temperatures, the growing conditions remain moist. Slowly growing trees are relatively small, and forest canopies are sparser and more open than in the south (Kersalo and Pirinen 2009). Scots pine (*Pinus sylvestris* L.) or Norway spruce (*Picea abies* (L.) Karst.) most often dominate the canopy in European northern boreal forests. Downy birch (*Betula pubescens* Ehrh.) and its subspecies mountain birch (*B. pubescens* ssp. *czerepanovii* (N.I.Orlova) Hämet-Ahti) are also common and may be the dominating tree species of a forest site. The understory vegetation typically consists of a layer of mosses and lichens (such as splendid feather moss (*Hylocomium splendens* (Hedw.) Schimp.), Shcreber's big red stem moss (*Pleurozium shcreberi* (Brid.) Mitt.), and *Polytrichum* moss (*Polytrichum* Hedw.); *Cladonia* lichen (*Cladonia* P. Browne), Iceland moss (*Cetraria islandica* (L.) Ach.), and a layer of ericaceous shrubs (such as crowberry (*Empetrum nigrum* ssp. *hermaphroditum* (Hagerup) Böcher) and *Vaccinium* spp. (L.)). The herb and grass layer is generally species-poor, with wavy hair-grass (*Deschampsia flexuosa* (L.) Trin.), hairy wood-rush (*Luzula pilosa* (L.) Willd.), and arctic starflower (*Trientalis europaea* L.)being common examples (Hotanen et al. 2008).

In northern regions, reindeer husbandry is an important livelihood. Reindeer graze freely in many areas, which can influence the number of broadleaved trees, particularly their seedlings and saplings (Kreutz et al. 2015). Lichen biomass and coverage have drastically decreased in areas where reindeer husbandry is carried out in Finland. Bryophytes have replaced many lichen species in forests where reindeer trampling and grazing occur (Väre et al. 1995; Susiluoto et al. 2008; Akujärvi et al. 2014). The forests are also used in multiple other ways. Large areas are protected, and despite the slow growth of trees, forests are used commercially. The recreation value of both commercial and protected forest areas is high. Plenty of hiking routes run through vast regions, and berry picking and hunting are also important forms of forest usage.

Northern Finland, and the northern forests, may experience alterations in the future because of land-use changes. Northern Finland has many mines along with potential places for establishing new mines. One of the promising ore deposits is a phosphate massif, which lies in Sokli, eastern Lapland. The Sokli phosphate ore consists mainly of apatite [$Ca_5(PO_4)_3F$] (Vartiainen and Paarma 1979), commonly used as an ingredient of phosphorus (P) fertilizers. Plans to open up a mine in Sokli have been alternating since the 1960s. Sokli is close to the Värriö Strict Nature Reserve, a protected area, where e.g. biological and air quality measurements have been conducted for decades. Sokli and Värriö are remote locations, and the air in the region is generally clean with barely any signs of pollution (Ruuskanen et al. 2003). The nearby Kola Peninsula in Russia is heavily industrialized with non-ferrous metal smelters of mainly nickel and copper (at Monchegorsk, Nikel, and Zapoljarnij), iron mines and mills (at Kovdor and Olenegorsk), apatite mines (at Apatite and Kirovsk), and an aluminum smelter (at Kandalaksha) (e.g. Paatero et al. 2008). The ecosystems surrounding the industrial plants are severely polluted, and e.g. forests in the immediate vicinity of the smelters in Monchegorsk have been completely destroyed and replaced with so-called industrial deserts (e.g. Tikkanen 1995; Paatero et al. 2008). During the last decades, the production rates have decreased and many improvements have been conducted to reduce aerial pollution (gaseous sulfur dioxide and nitrogen dioxide and particle-bound metals such as arsenic, nickel, and copper) from the industry (Paatero et al. 2008). Nevertheless, the industry in Kola is still a source of pollution to the Peninsula and to some extent to Finnish Lapland. If the wind blows from the direction of Kola, higher quantities of pollutants are detected in the air at Värriö. However, this only happens occasionally and temporarily (Ruuskanen et al. 2003; Kyrö et al. 2014). The Sokli phosphate mine would be an open-pit mine (Pöyry Environment 2009). Such mines can cause the aerial deposition of phosphates and heavy metals into surrounding ecosystems (Reta et al. 2018). The material from the mine would be transported elsewhere by trucks for further processing (Pöyry Environment 2009). Thus, traffic pollution in the region would increase remarkably compared to the current situation.

In addition to land-use change, climate change affects the northern region of Finland. Climate change is predicted to be stronger and faster in northern latitudes than in the more southern locations (Kurtz et al. 2008; Hartmann et al. 2013). The reason for this is a process called Arctic amplification, which is a characteristic feature of the Earth’s climate system and is expected to become stronger in upcoming decades (e.g. Serreze and Barry 2011). Because of Arctic amplification, the temperature rise in the Arctic (67° N to 90° N) is expected to be approximately 2 °C higher than elsewhere on the globe (Hartmann et al. 2013). Several other places in addition to Sokli in northern Finland have ore deposits, where new mines are being planned. Thus, large-scale changes due to land use and climate are expected to occur in the northern boreal region of Finland in upcoming decades. To be able to predict and be prepared for such changes, it is of utmost importance to assess what the baseline situation is.

1.2. Soil nutrients and their interactions with vegetation and atmosphere

Plants need many nutrients for growth and maintenance, but the most important ones are usually nitrogen (N) and P, whose shortages can limit growth (Koerselman and Meuleman 1996). Boreal forests on mineral soils are generally limited by N (Tamm 1991), and tree growth usually increases when fertilized with N (Saarsalmi and Mälkönen 2001). Atmospheric deposition of N can act as a fertilizer in boreal forests (e.g. Korhonen et al. 2013). The annual N deposition to forests is 3–4 kg/ha in southern Finland and 1–2 kg/ha in northern Finland. These are low values compared to Central and Southern Europe, where the annual deposition of N can, at its highest, be as much as 30 kg/ha (Dirnböck et al. 2013). Excess amounts of nutrients have been linked with a decreased number of plant species in polluted regions experiencing heavy atmospheric N deposition (Dupré et al. 2002; Dirnböck et al. 2014). Plants use N for building up proteins (Marschner 1995). According to current knowledge, plants can directly utilize only certain forms of N. These forms are inorganic ammonium (NH^{4+}), nitrate (NO^{3-}) (e.g. Marschner 1995; Kielland et al. 2007), and organic amino acids (Kielland et al. 2007; Näsholm et al. 2008). These forms are available only in limited amounts in soil, and most of the N is bound in organic material (Marschner 1995).

Some plants, for example legumes, have specific nodules in their roots, with bacteria that can fix N_2 directly from the atmosphere (Marschner 1995).

Single limitation by P in boreal forests on mineral soil has not been detected, but P limitation is possible on boreal peatlands due to slow mineralization (Brække and Salih 2002; Moilanen et al. 2010) and poor access to the underlying mineral soil (Shaver et al. 1998). Soil also holds P tightly, and very often it is the least mobile major nutrient for plants. Plants can take up P mostly as inorganic phosphates (Pi) H_2PO^{-4} and $HPO_2{}^{-4}$, also called soluble P. Soluble P is derived from primary minerals (e.g. apatite) by weathering, secondary minerals (e.g. Ca and Fe phosphates), via dissolution, and from P sorbed on mineral surfaces (e.g. clay, carbonates, Fe, and Al oxides) via desorption. Additionally, P is mineralized from decomposing organic matter (Marschner 1995; Hinsinger 2001). Plants need P particularly during their early development, and use it in various processes such as photosynthesis and respiration. Plants that are able to fix N_2 directly from the atmosphere need P for N fixation. Insufficient P causes problems with leaf development, and the number and size of leaves in a plant suffering from P deficit remain small (Marschner 1995; Raghothama 1999). Phosphates also act as building blocks for several important metabolites such as adenosine triphosphate, phospholipids, and nucleic acids (Marschner 1995; Raghothama 1999; Vance et al. 2003). Thus, P deficiency is a strongly limiting factor for plant growth even in otherwise favorable conditions. The co-limitation of N and P is common in many types of forests, and the ratio of these two nutrients is generally very important worldwide (Vadeboncoeur 2010; Augusto et al. 2017). For example, the addition of NP fertilizer to a temperate forest site in southern Sweden led to a doubling of vascular plant species richness (Hedwall et al. 2017). This effect was only seen when N and P were added together.

Nutrient availability in soil and the utilization of nutrients by plants are critical information for understanding processes in forest ecosystems (Merilä and Derome 2008). Understory vegetation, soil nutrients, and the local climate are important parts of a forest ecosystem and connect with each other in several ways. For example, soil nutrients and the climate affect vegetation species composition, and the growth and chemical composition of the vegetation. Species composition concurrently interacts with soil nutrients, as e.g. the mineralization rate of carbon (C) or N can vary under different plant species (Vinton and Burke 1995). While nutrient release in current conditions in northern boreal forests is slow, increased soil temperature induced by a warmer climate may speed up the processes in the future. Faster decomposition rates may increase the mineralization of both N and P from dead organic material. Climatic factors may affect the release of N more than P, at least in places where P availability is more dependent on the parent material of soil and landforms (Augusto et al. 2017). The global cycles of N, P, and C are interconnected (Figure 1), and changes in one can cause variation in the others, and thus re-shape vegetation. Understory vegetation in northern or high-altitude regions has already undergone changes, as increased temperature has caused the expansion of shrub cover in subarctic mountains in Sweden (Havstrom et al. 1992; Wilson and Nilsson 2009), high Arctic heath in Svalbard (Havström et al. 1993), Arctic tundra in Alaska (Chapin III et al. 1995; Hobbie and Chapin III 1998; Sturm et al. 2001) and elsewhere in the Arctic (Dormann and Woodin 2002; Walker et al. 206), meadows in the Rocky Mountains (Harte and Shaw 1995), and dwarf shrub heath in Iceland (Jónsdóttir et al. 2005). An increase in growth is often linked with the amount of available nutrients, which are crucial for growth (Jónsdóttir et al. 2005; van Wijk et al. 2003).

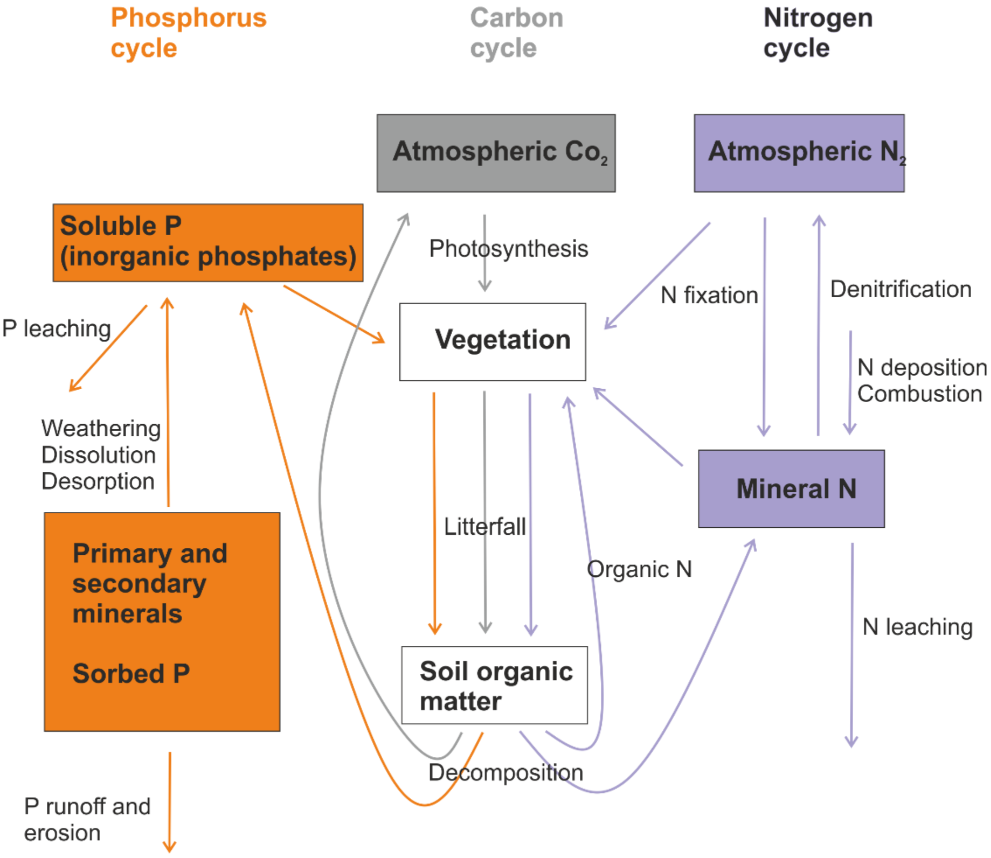
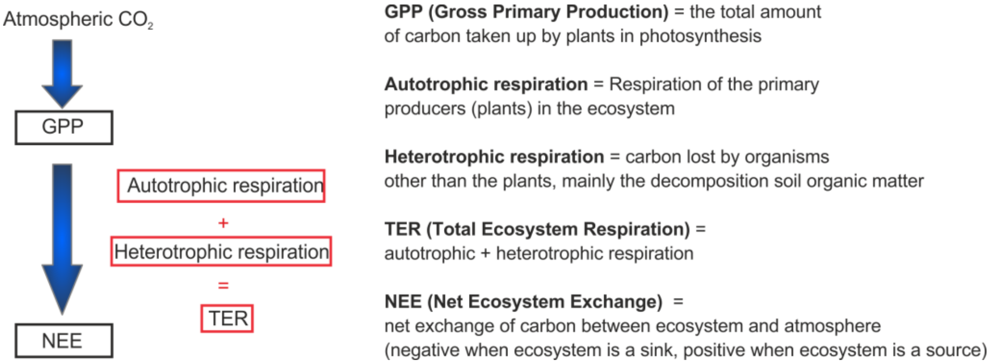


Figure 1. The global biogeochemical cycles of phosphorus (P, orange), carbon (C, gray), and nitrogen (N, purple) are interconnected. Modified from Llado et al. 2017.

1.3 Forest-atmosphere interactions and climate change

The importance of forests in the global C cycle is undeniable. Forests form both a notable sink of atmospheric C along with a C storage. A sink of C is a reservoir, which binds more atmospheric C than it releases. A C source is the opposite; a reservoir that releases more C than what it stores. A C storage is an entity that sequesters atmospheric C, such as living and dead plant biomass and soil. In boreal forests, the largest C storage lies in the soil (Pan et al. 2011) due to slow decomposition rates. Soil texture and nutrient availability affect how efficiently forests can bind atmospheric carbon dioxide (CO_2). The understory vegetation may have an important role in the C dynamics of a forest, especially if the canopy is sparse (Kulmala et al. 2011; Hari et al. 2013) such as in northern boreal forests. The gross primary production (GPP) of the understory in the boreal forest ecosystem may be as much as 60% of the GPP of the whole site (Ikawa et al. 2015). Gross primary production basically equals the photosynthesis of the forest site, as it is the total amount of CO_2 taken up by plants during photosynthesis (Figure 2). In addition to photosynthesis, plants also respire in a process that is inverse to photosynthesis. Plant respiration is called autotrophic respiration, which can be divided into maintenance respiration and growth respiration. Maintenance respiration depends on biological activity, which increases with temperature and is highest in tissues with high metabolic rates (Ryan 1991). Growth respiration is proportional to growth (Amthor 2000). When it is dark, plants only respire, while they both respire and photosynthesize when light is available. Temperature drives both photosynthesis and respiration, but respiration is more sensitive to temperature changes than photosynthesis is (Ryan 1991). The balance between respiration and photosynthesis may be modified by climate change, as the same environmental drivers cause different impacts (DeLucia et al. 2007).

In northern boreal forests, the current growing conditions have prevailed for many millennia. However, notable changes will likely occur in this area because of climate change. Rising mean annual temperatures, prolonged growing seasons, and increased precipitation rates are expected and have already happened in northern regions (e.g. Hartmann et al. 2013; Peñuelas et al. 2020). In addition to these more general changes in growing conditions, extreme weather events are expected to become more frequent than currently (e.g. Beniston 2004; Hartmann et al. 2013). Such events include drought, heat, heavy rain, and frost in the summertime, which may all have negative impacts on the forest ecosystems and their CO_2 and water (H_2O) exchange. Water also circulates between the vegetation and atmosphere. While taking in CO_2 through their open stomata, plants simultaneously release H_2O to the atmosphere. To replace the resulting loss, plants need to absorb H_2O from the soil. The release of water to the atmosphere is called transpiration. The term evapotranspiration (ET) is used when plant transpiration is combined with the evaporation of water from different surfaces in the forest.



GPP (Gross Primary Production) = the total amount of carbon taken up by plants in photosynthesis

Autotrophic respiration = Respiration of the primary producers (plants) in the ecosystem

Heterotrophic respiration = carbon lost by organisms other than the plants, mainly the decomposition soil organic matter

TER (Total Ecosystem Respiration) = autotrophic + heterotrophic respiration

NEE (Net Ecosystem Exchange) = net exchange of carbon between ecosystem and atmosphere (negative when ecosystem is a sink, positive when ecosystem is a source)

Figure 2. The terms and concepts related to the carbon dioxide (CO_2) exchange between ecosystem and the atmosphere. (Modified from Kalliokoski et al. 2019).

Scots pine, Norway spruce, and their understory vegetation grow in different nutrient and hydrological conditions and may therefore react differently to forthcoming changes. Norway spruce is known to be more prone to drought than Scots pine (e.g. Lebourgeois et al. 2010; Lebourgeois et al. 2012; Eilmann and Rigling 2012; Lévesque et al. 2013;, van der Maaten-Theunissen et al. 2013; Baumgarten et al. 2019), and also more sensitive to frost than Scots pine (Lundmark and Hällgren 1987; Linkosalo 2014). Frost during the growing season can damage the leaves and reduce their greenness (Gu et al. 2008; Linkosalmi et al. 2016). Droughts are uncommon in northern regions; instead, precipitation and soil moisture are generally considered sufficient for growth. However, a tree-ring study from a northern boreal forest in Finland showed that Scots pine and Norway spruce growth had decreased during dry years (Aakala et al. 2018). The same happened with white spruce (*Picea glauca* (Moench) Voss) in Alaska (Barber et al. 2000; Wilmking et al. 2004). At least further south, drought has apparently caused remarkable changes in CO_2 flux rates. During a drought in 2003, GPP decreased in many parts of Central and Southern Europe (Ciais et al. 2005) and Northern Europe was also affected during a drought in 2006. For example, the 2006 drought led to the GPP and ET rates of a Scots pine forest to decrease strongly in southern Finland (Gao et al. 2016; Gao et al. 2017). When the climate warms, such phenomena could also occur further in the north. In many forest ecosystems, the respiration rate of plants (i.e. autotrophic respiration) increases with rising temperature, which may cause negative impacts on the C balance of plants (Jones et al. 1998). The decomposition of organic matter, i.e. heterotrophic respiration, also depends on temperature (Davidson and Janssens 2006). High temperatures may amplify the rate of decomposition and turn northern soils from a C sink to a C source (Crowther et al. 2016). However, certain soil microbes suffer in dry conditions, and drought may inhibit their functioning (Moyano et al. 2013; Sierra et al. 2015). Nevertheless, some changes will likely occur in decomposition rates, possibly reducing ecosystem respiration. These changes may also affect the release of soil nutrients, which in turn affects vegetation, followed by variation in CO_2 exchange.

2. AIM OF THE STUDY

In this dissertation, I aim to analyze and characterize the baseline status and the future aspects of northern boreal forest vegetation in Finland to assess the resilience of structure and CO_2 sink in changing conditions. My objectives are to 1) identify the connections between soil N and P content and forest vegetation, 2) quantify the relationship between all forest vegetation and atmosphere considering the CO_2 flux between them, and 3) based on the above, discuss how climate change will affect northern boreal forests in terms of vegetation, nutrient cycling, and CO_2 flux dynamics.

More specifically, with the help of the three sub-studies included in this dissertation, I aim to answer the following questions:

Question 1 (Q1): What is the relationship of soil total N and P content with vegetation cover composition in a northern boreal forest located near a phosphate massif?

Question 2 (Q2): What is the role of understory vegetation in the CO_2 flux dynamics of a northern boreal Scots pine forest?

Question 3 (Q3): How resilient are the CO_2 exchange rates of northern boreal forests to extreme weather events and climate change?

Question 4 (Q4): Will the nutrient dynamics and the composition of plant species change in northern boreal forests in the future?

For this purpose, I studied three forest areas in Finnish Lapland: the surroundings of the Sokli phosphate massif near Värriö (easten Lapland) (Article **I**) and a Scots pine site in Värriö both alone (Article **II**) and in comparison with the Kenttärova Norway spruce site in Pallas (western Lapland) (Article **III**).

3. METHODS

3.1 Study sites

All three articles used data measured at or in the surroundings of Värriö Subarctic Research Station (67° 44′ N, 29° 36′ E) in eastern Lapland in Finland. In article **I**, we had 16 study plots (Figure 3), which were located in the surroundings of Sokli phosphate ore mine (67° 48′ N, 29° 16′ E). Each of these plots was 30 × 30 m^2 in size, and they included twelve sub-plots per plot for observing the understory vegetation and coring soil samples. These plots had Scots pine, Norway spruce and downy birch as the main tree species. Some plots had a mixed composition of all three species. In article **II**, we used data from the Station for Measuring Ecosystem-Atmosphere Relations (SMEAR I station, 67° 46′ N, 29° 35′ E), which is located at the Värriö Research Station. The mean annual temperature and mean annual precipitation are -0.5 °C and 601 mm, respectively (Pirinen et al. 2012). The site is a Scots pine forest located 400 m above sea level. The understory vegetation at the SMEAR I station is very typical for the region: a combination of mosses and lichen, such as Schreber's big red moss, broom fork-moss (*Dicranum scoparium* Hedw.), and reindeer lichen (*Cladonia rangiferina* (L.) F. H. Wigg.*)*, along with dwarf shrubs, most commonly bilberry (*Vaccinium myrtillus* L.*)*, lingonberry (*Vaccinium vitis-idaea* L.*)*, and crowberry Soil type is haplic podzol with sandy tills (FAO 1988), similarly to the soils at the plots in article **I**. The understory vegetation of the plots in article **I** was relatively variable and will be discussed in section 4.

In article **III,** we used data from SMEAR I, and Kenttärova forest (67° 59′ N, 24° 15′ E), which is located at the Pallas Atmosphere-Ecosystem Supersite hosted by the Finnish Meteorological Institute (FMI) (Figure 3). The mean annual temperature at the site is -1.0°C and mean annual precipitation sum is 521 mm (Pirinen et al. 2012). The Kenttärova site is a Norway spruce forest with some downy birch, Eurasian aspen (*Populus tremula* L.), and goat willow (*Salix caprea* L.) growing as mixed species. The forest is located 347 m above sea level on a hilltop plateau, which is circa 60 m above the surrounding planes (Aurela et al. 2015). The understory at Kenttärova mainly consists of mosses, such as Schreber's big red moss, splendid feather moss, and rugose fork-moss (*Dicranum polysetum* Sw.), and dwarf shrubs bilberry, crowberry and lingonberry. Soil type is podzolic till (Aurela et al. 2015).

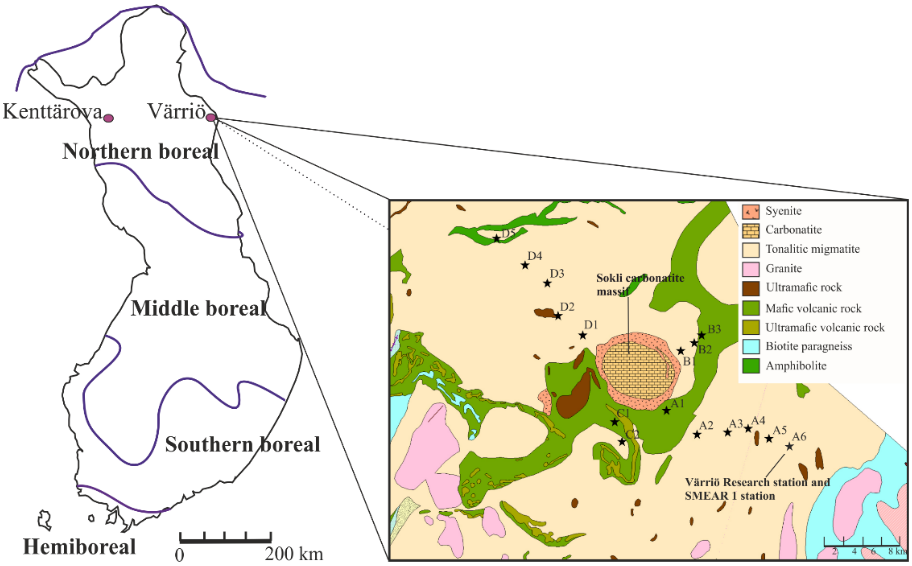


Figure 3. The boreal subzones (according to Hämet-Ahti 1981) and locations of Värriö pine site and Kenttärova spruce site on the left. The study plots used for article **I** are shown in the geological map.

3.2 Measurements and laboratory analyses

*3.2.1 Field measurements (Articles **I–III**)*

The field measurements focused on the features of vegetation and soil nutrient contents, and momentary fluxes of CO_2 and H_2O. Figure 4 illustrates the three articles and some of the methods used in them. The understory vegetation survey was conducted by setting a square frame of 1m^2 onto the ground, recording all the plant species within the frame, and visually estimating their approximate projection cover (percentage of surface). Four soil samples were taken next to each vegetation square with a corer (diameter 5 cm), so that the maximum distance of the sample was 1 m away from the square (Liski 1995). The maximum depth of the samples was approximately 15 cm, as the soil layers were very shallow, and in places it was hard to core the samples because of the rocky soil. Due to lack of laboratory space and resources at the site, the soil samples were divided into different soil horizons directly after sampling. We used the same definitions for the soil horizons as Köster et al. (2014). Thus, the four soil horizons were F (litter layer), O (humus), A (eluvial layer), and B (illuvial layer). After separation of the horizons, we had four samples of each horizon from each sub-plot. These were pooled to form one composite sample per horizon per sub-plot. In the study, we also measured the heights and diameters (diameter at a height of 1.3 m) of all trees inside the 900-m^2 area and took needle/leaf samples from conifers (five trees per species) and birches (fresh and litter leaves). More detailed information of the study setup and fieldwork is in article **I**.

Carbon and H_2O flux measurements (**II** and **III**) were based on the eddy covariance (EC) method. The necessary devices for EC were set up in towers above the canopy at both the SMEAR I and Kenttärova sites. The scale in these measurements is the whole ecosystem, thus the trees, understory, and soil were all included. Article **II** included, in addition, flux data from a sub-canopy EC system and soil chambers from Värriö, while article **III** included cuvette (shoot chamber) flux data from Värriö and EC data from the Kenttärova site in Pallas. Especially in studies **II** and **III**, we utilized data from meteorological measurements, mainly from the FMI measurement sites at Värriö Subarctic Research Station and at Alamuonio near Kenttärova. A detailed explanation of the flux and meteorological measurements can be found in articles **II** and **III**.

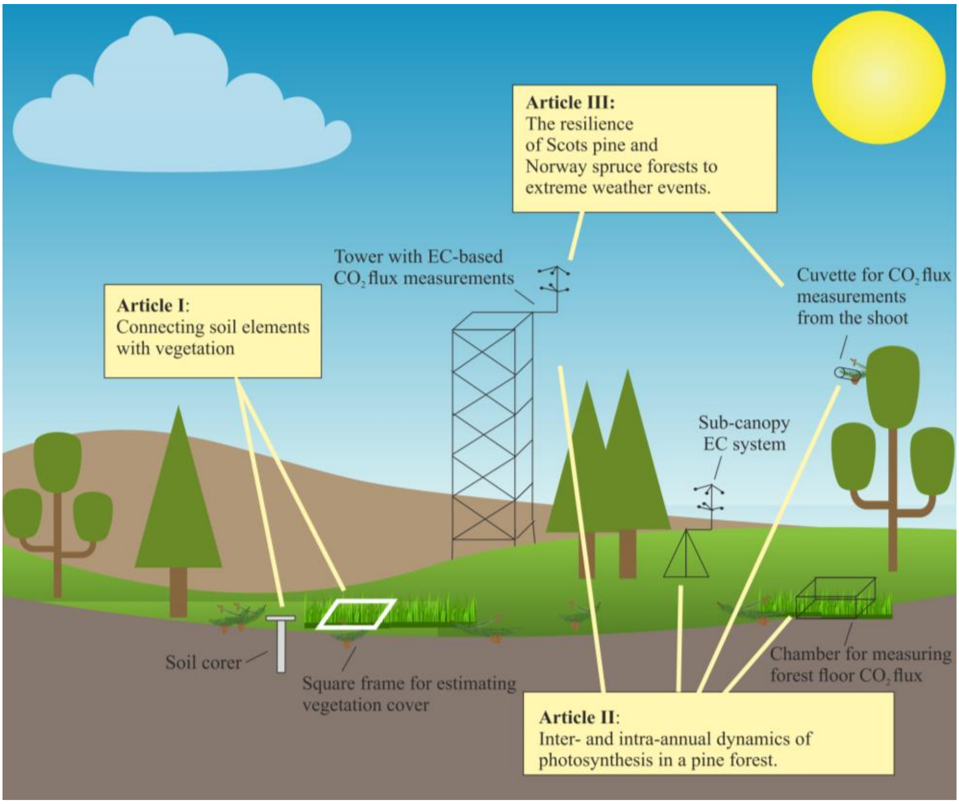


Figure 4. The three articles in this thesis, and their most important measurement methods.

*3.2.2 Laboratory analyses (Article **I**)*

The soil samples from mineral soil layers A and B were air-dried and the samples from the organic F and O layers were dried at 60°C for 48 hours on-site. The samples were stored as dried for a couple of months, after which the mineral soil layers were sieved with a 2-mm sieve, and the organic samples were milled before storing them again in a dry place for further analyses. The needle and broadleaf samples were dried at 60°C for 48 hours. After this, the samples were stored in a dry place for further analyses. Later on, all the samples were wet combusted (details in article **I**) and the resulting extracts were analyzed for their total elemental concentrations (P) by inductively coupled plasma optical emission spectrometry. I also analyzed total C and N directly from the sieved and milled soil, and leaf and needle samples with an element analyzer, which uses a high-temperature combustion method with subsequent gas analysis of C and N (VarioMax, Elementar Analysensysteme GmbH, Germany). I analyzed pH from the O layer from a suspension where the sample was mixed with ultrapure water. Details of the analyses can be found in article **I**.

*3.2.3 Data analyses (Articles **I–III**)*

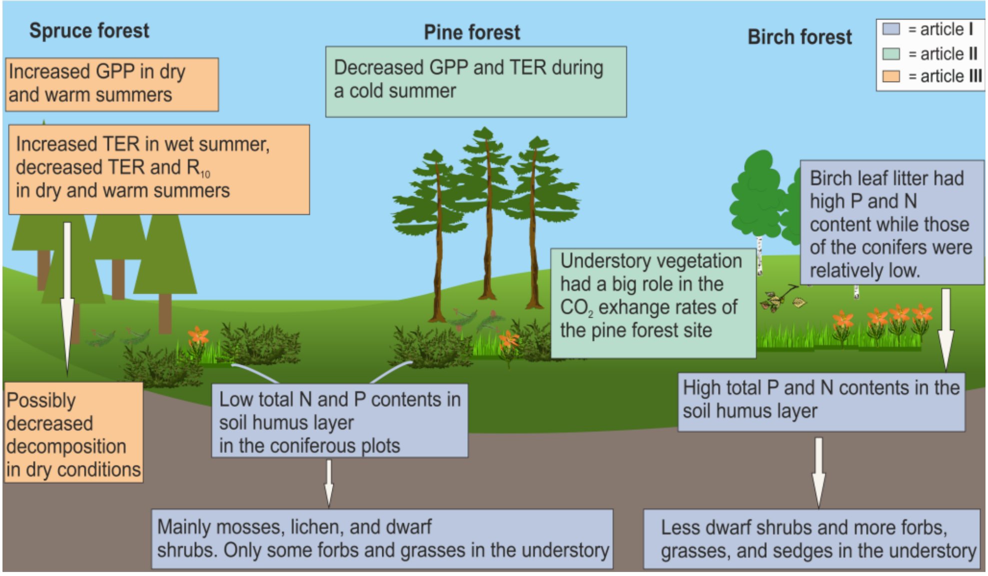
In article **I,** we utilized linear mixed-effect models for quantifying which factors (dominant tree species, tree age, rock parent material, soil layer) affect the soil nutrient content the most. We used non-metric multidimensional scaling for ordinating the plots based on their average understory vegetation cover (% of soil surface) (Minchin 1987). We then fit vectors of different environmental factors (nutrient contents in the humus layer, volume of birch) to see their relationship with the ordination pattern. We also used one-way analysis of variance (ANOVA) to compare the needle nutrient contents in different age groups and between the research plots. All these analyses were performed in R programme 3.4.3 (R Development Core Team, 2017), and the detailed information with all the used R packages are in article **I**.

Article **II** describes the data processing and calculations needed for the EC data in articles **II** and **III**. This processing includes gap-filling of the data by modeling the photosynthesis and respiration with a set of parameters derived from available observations together with measured temperatures of air and soil. We additionally used the optimal stomatal control model (Hari and Mäkelä 2003; Kolari et al. 2007) and the Stand Photosynthesis Program (Mäkelä et al. 2006) to help estimate the photosynthesis of a canopy from shoot flux data. The downscaled GPP of the understory was calculated as a difference between the GPP of the whole ecosystem (from EC) and the estimate of canopy photosynthesis. Understory photosynthesis was also calculated in another way by upscaling it from modeled species-specific photosynthesis rates of vascular plants. From the difference of the EC-derived GPP and the upscaled photosynthesis of the understory, we obtained another estimate for tree canopy photosynthesis. We thus had upscaled and downscaled versions for both the canopy and the understory photosynthesis. We used data from 2012–2015 in article **II**.

In article **III**, we used long-term meteorological data (from 1981–2010) and compared it with meteorological data from the study years. These study years were 2012–2018 for Värriö pine forest and 2003–2013 for Kenttärova spruce forest. We calculated R_{10} and P_{1200} (normalized respiration at a constant temperature of 10°C and photosynthesis at constant photosynthetically active radiation (PAR) of 1200 μmol m^{-2} s^{-1}, respectively) from the EC data and photosynthetic capacity β from the pine shoot flux data. We also calculated the ratio of ET/vapor pressure deficit (VPD). We utilized one-way ANOVA to compare summertime values of TER, GPP, R_{10}, and P_{1200} between the study years. A more detailed description of the calculations is in article **III**.

4. RESULTS AND DISCUSSION

In chapter 4.1, I will answer **Q1**–**Q3** by going through the most important results of articles **I–III** (illustrated in Figure 5) and discussing them in relation to the existing literature. In chapter 4.2, I discuss what is suggested to happen to northern boreal forest vegetation in the future (**Q4**).



Increased GPP in dry and warm summers

Increased TER in wet summer, decreased TER and R_{10} in dry and warm summers

Possibly decreased decomposition in dry conditions

Decreased GPP and TER during a cold summer

Understory vegetation had a big role in the CO_2 exhange rates of the pine forest site

Low total N and P contents in soil humus layer in the coniferous plots

Mainly mosses, lichen, and dwarf shrubs. Only some forbs and grasses in the understory

Birch leaf litter had high P and N content while those of the conifers were relatively low.

High total P and N contents in the soil humus layer

Less dwarf shrubs and more forbs, grasses, and sedges in the understory

Figure 5. The main results of the articles in this dissertation. Box color describes the source article. Data for spruce forest were from 2003–2013 and for pine forest from 2012–2018.

4.1 The baseline status of soil-vegetation-atmosphere interactions in northern boreal forests (Q1–Q3)

My first research question (**Q1**) dealt with the connection of soil N and P contents with vegetation cover in northern boreal forests near a phosphate massif. The contents of these nutrients are important for forest vegetation, especially in the organic layers of soil where the roots of the understory vegetation grow. Most nutrient studies from boreal forests have focused on N, because of its growth-limiting role. Several fertilization studies have shown that addition of N changes the understory species composition in boreal forests (Mäkipää 1999; Strengbom et al. 2002; Gundale et al. 2014). Similarly, Salemaa et al. (2008) found that the number of vascular plant species (grasses and forbs) in boreal forests increased together with increasing N content in the organic soil layer. Their study covered several forest sites across Finland. However, in Arctic, subarctic, and alpine tundra ecosystems, P may co-limit or limit plant production (Shaver and Chapin 1995; Aerts and Chapin 1999; Seastedt and Vaccaro 2001; Hobbie and Gough 2002; Soudzilovskaia et al. 2005; Giesler et al. 2012). Both the weathering and mineralization of P may be restricted because of the cold climate in the tundra (Stark 2007). In addition, certain microorganisms in tundra soil need P and thus may compete with plants in P uptake (Jonasson et al. 1999). Arnesen et al. (2007) found that the availability of P in the soil together with pH and carbonate contents correlated the best with alpine vegetation on exposed rocky habitats in northern Norway. They found that the diversity of vascular plants increased with higher P availability. We found evidence of the importance of soil P content in northern boreal forests, albeit our site was very special because of the Sokli carbonatite massif (**I**). Our results showed that both N and P contents in the humus layer were important in explaining the community composition of understory vegetation in northern boreal forests (Figure 5). Humus P content seemed even more important than N content, and the coverage (% of surface) of species preferring more fertile growing conditions (forbs, grasses, and sedges) increased almost linearly with it. Salemaa et al. (2008) also found that extractable soil P had a higher importance for vegetation patterns in the north than in southern Finland, which supports our finding.

The understory vegetation in the plots of article **I** consisted of common Finnish forest species (Reinikainen et al. 2000). At most plots, the vegetation cover was typical for the most common forest site types in the region (Cajander 1909, 1949; Hotanen et al. 2008). The understory consisted of mosses (e.g. Schreber’s big red stem moss), lichen (e.g. *Cladonia* spp.) and dwarf shrubs (e.g. bilberry, crowberry), whereas Norway spruce or Scots pine were the dominating tree species. However, in some plots downy birch was the dominant tree species and the understory had a higher number and coverage of forbs, grasses, and sedges (such as wood small-reed (*Calamagrostis epigejos* (L.) Roth), sedges (*Carex* L.), Arctic raspberry (*Rubus arcticus* L.), and hairy wood-rush). These plots also had high N and P contents in the humus layer. Although the needle and broadleaf contents of N and P did not differ significantly between the plots, tree species was important for the nutrient dynamics of the research plots. The results of the mixed-effect model showed that the dominating tree species (Scots pine, Norway spruce, or downy birch) together with soil layer (P content in the different layers) were the most important factors explaining soil P content. When we inserted birch as the dominant tree species and F layer P content into the model, it explained 45% of the total soil P content (data from all layers were considered).This was the most explanatory model of all. For soil total N content and soil C:N ratio in all layers, soil horizon was the most important factor explaining 20% of both. The best estimates of N were obtained with F as the soil horizon. Our results suggest that birch, with its high annual input of leaf litter, forms an important source of P to the soil. Supporting this, experimental studies have reported that adding birch leaf litter increased the total and available content of P in the soil (Rinnan et al. 2008; Sorensen and Michelsen 2011).

What comes to **Q2**, our results (**II**) found that the role of the understory vegetation in stand photosynthesis was high at the Scots pine site. It accounted for 43% to 49% of the annual whole ecosystem photosynthesis, depending on the year. A high proportion (61%) of understory in the stand photosynthesis was also reported from an Alaskan black spruce (*Picea mariana* Mill.) forest with an open canopy (Ikawa et al. 2015). Studies from more southern boreal forests with higher canopy covers have reported understory shares ranging from 10% to 20% (Swanson and Flanagan 2001; Kolari et al. 2006; Ilvesniemi et al. 2009; Bergeron et al. 2009). Differences also exist between the compartments of a forest site regarding their annual dynamics. The canopy photosynthesis rate in the Värriö Scots pine forest began increasing about a month before snowmelt (**II**). Thus, the understory was still under snow cover when the canopy experienced its spring awakening. Many models related to primary production do not take snow cover into account, and for that reason, may not accurately estimate the production of forests with open canopies. The Värriö pine forest was a CO_2 sink from around mid-May to early September. Rainy days sometimes caused the forest to turn into a source of CO_2 also during the summer. This occurred especially in summer 2015, when the weather was cloudy and rainy throughout the summer and the PAR level was too low for efficient photosynthesis. In the short term (2012–2015), GPP seemed to have a higher response to temperature sum than TER (**II**). This trend remained similar, although it evened out when three more study years (2016–2018) were included (Figure 6). These findings are similar to previous studies (Law et al. 2002, Mäkelä et al. 2008). Contrariwise, such a clear connection between temperature sum and GPP and TER did not exist in Kenttärova spruce forest (Figure 6). Other factors, such as soil drying, may restrain GPP and TER once the temperature sum is high enough.

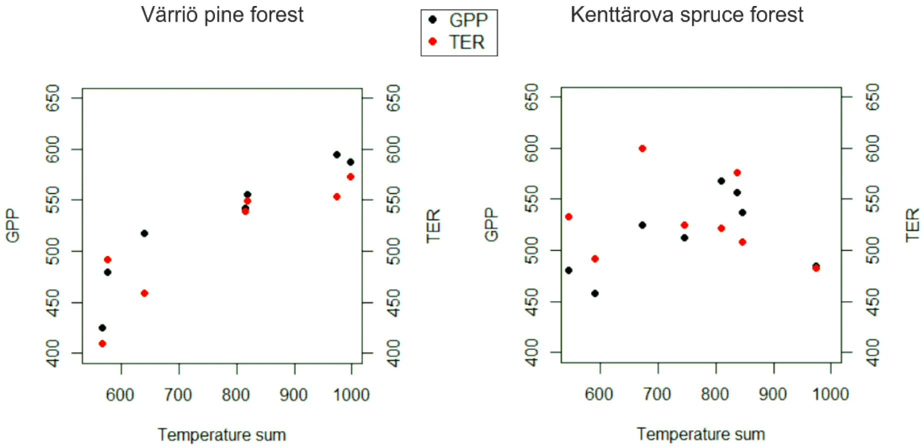


Figure 6. Annual GPP and TER (g C m^{-2} yr^{-1}) over cumulative temperature sums (the unit is °C and a 5°C threshold was used) from Värriö pine forest and Kenttärova spruce forest site. Some data were missing from Kenttärova and thus the years 2007, 2009, and 2010 are missing from the figure.

It is normal for northern boreal forests to experience summer conditions varying from cold to relatively warm and everything in between. This is visible, for example, in the variation of temperature sums between the years in Värriö and Kenttärova (Figure 6). As we discovered (**II** and **III**), the variation in CO_2 fluxes between the forests and atmosphere can be high between the years. Some of the summer seasons at our Scots pine and Norway spruce sites were so different from the long-term average (30 years of data) in terms of temperature or rainfall, that they fulfilled the IPCC definition for statistically extreme (Seneviratne et al. 2012) (**III**). The statistical definition is a good starting point for defining extreme events, but sometimes ecosystems may respond extremely even though the statistical criteria are not met (Gutschick and BassiriRad 2003; Smith 2011). In our findings, only the Värriö pine forest had extremely warm or dry summers in statistical terms. However, the effects of warm and dry conditions in both the measured and modeled CO_2 flux rates were more visible from the Kenttärova spruce forest. Kenttärova spruce forest seemed less resilient against extreme events than the Värriö pine forest. Both the measured and modeled respiration (TER and R_{10}, respectively) rates decreased during a period of July–August in the dry and hot years compared to other study years (Figure 6). The GPP, on the other hand, increased during the dry and warm years in both forests (**II** and **III**). For this reason, and because TER significantly increased during a wet summer, the decrease of TER values during dry and warm summers was apparently caused by lowered decomposition of soil organic matter. This implies that predictions estimating that all northern forest soils will turn into C sources because of climate warming seem slightly exaggerated. The H_2O flux rates from forests also depend on temperature. Some climate models have predicted that amplified ET may outweigh the predicted increase in precipitation and cause intermediate drying of soil in boreal forests (Ruosteenoja et al. 2017). Our study did not find evidence of anything like this, as the H_2O fluxes or the ratio of ET/VPD of the spruce or pine forests did not differ between years (**III**).

Cold spells may occur if a spring is warmer than usual and a frost follows after the vegetation has already started growing and photosynthesizing. Such cold spells have been found to cause remarkable damage to vegetation. In eastern US, a freezing period after an exceptionally warm spring led to crop plant mortality and severe damage to tree leaves (Gu et al. 2008). The greenness of plants was remarkably reduced. The vegetation in northern boreal forests is considered to be rather resistant towards coldness. After all, the growing conditions are relatively cold and the growing seasons short (e.g. Pirinen et al. 2012). However, a cold spell occurred around mid-summer 2014, which showed that reduced leaf greenness also occurs in the north (Linkosalmi et al. 2016). During this same cold spell in 2014, which lasted for 11 days in Värriö, we saw a temporary dip in the photosynthetic capacity β of pine shoots. When the cold spell was over, β increased together with temperature. This implies that the cold spell was either not harsh enough to cause severe damages or the vegetation was very resilient towards such spells. A cold summer reduced the GPP and TER rates of the Scots pine forest compared to other study years. The year following the cold one was extremely warm, and the forest photosynthesized with record high values. This implies that the cold summer did not damage the vegetation, for example the buds, which form in fall. Similarly, photosynthesis and respiration of the spruce forest returned to their average levels after the dry years, implying that at least the trees were not harmed (**Q3**).

4.2 Northern boreal forest vegetation in the future (Q4)

Northern forest ecosystems are often described as vulnerable to climate change, which is amplified at high latitudes (Kurtz et al. 2008; Hartmann et al. 2013). Local variation in the consequences of climate change may be high, and most forest processes are interconnected. Thus, it is not easy to say exactly what kind of effects climate change will cause on forest vegetation. However, several experimental and modeling studies have tackled the issue, and their results shed some light to what may take place in the future. According to simulations related to the effects of climate change on forest biodiversity in Finland (Kellomäki et al. 2005, 2008), species richness (number of species) may increase in the north of the country. This occurs if decomposition of organic matter increases and the release of nutrients speeds up, leading to increased productivity of forestland. On the other hand, species that currently grow at high latitudes seem to suffer the greatest losses (Skov and Svenning 2004) and shifts in tree species and their compositions are expected (Sykes et al. 1996; Thuiller 2003). According to other modeling predictions (Bakkenes et al. 2002), over 90% of the currently occurring higher plants should maintain their distribution in a 50-year time span, although regional extinctions may occur (Sætersdal et al. 1998). Specialist species will likely suffer and those that are able to grow in various conditions will benefit from the situation. Next, I will take a closer look at the reasons causing the changes in vegetation that I described in this section.

Warmer temperatures may affect vegetal growth and the CO_2 exchange between vegetation and the atmosphere. Northern boreal forest ecosystems are on the edge of the northern forest line and are generally considered to be sink-limited so that tree growth depends on temperature (Körner 2003). Previous studies have reported that with increasing temperature, forests in the north will likely benefit and increase their growth (e.g. Nemani et al. 2003; Boisvenue and Running 2006; Lindner et al. 2010). We showed that warm weather caused the forests at Värriö (**II** and **III**) and Kenttärova (**III**) to photosynthesize at high rates. The results from article **II** also imply that the dwarf shrub-dominated ground vegetation of a Scots pine site begins photosynthesizing more when the temperature is higher.

Rising air temperatures can lead to warmer soil temperatures. This can cause higher microbial activity, faster decomposition rates, and nutrient circulation, as e.g. N mineralization should speed up in warmer conditions (Rustad et al. 2001; Robinson 2002). In certain cases, soil warming may decrease the amount of available soil water, which can hinder soil microbial activity and slow down decomposition rates (Sjögersten and Wookey 2004; Hicks Pries et al. 2013). As mentioned, this could have been the case in Kenttärova spruce forest, where the slower decomposition rates may be one reason for the decrease in TER during warm and dry summers (**III**). In the course of climate change, the frequency of extreme weather events is expected to become higher than currently. We may thus expect more extremely warm summers, which may cause a decrease in TER, especially in northern Norway spruce forests. The understory species of spruce forests may be more susceptible to droughts than the species growing in Scots pine forests. For example, bilberry, which is very common in spruce forests, has been found to recover slower from drought than lingonberry, which is more common in pine forests and drier sites (Ganthaler and Mayr 2015; Palmroth et al. 2019).

Shrub cover increases in Arctic regions with a warming climate (Bret-Harte et al. 2001; Sturm et al. 2001; Walker et al. 2006; Park et al. 2016). Walker et al. (2006) observed that the height of graminoids, forbs, and shrubs along with the dominance of woody plants increased with warming at treeless high and low Arctic and alpine ecosystems. As several studies have found, climate warming has, to some extent, corresponding effects on vegetation as nutrient addition. This is likely because it causes increased nutrient mineralization in some ecosystems. Increased N mineralization may in turn boost plant growth (Hobbie et al. 2002; Robinson 2002). For example, the production and biomass of woody shrubs increased after N and P fertilization at a moist tundra site in Alaska (Chapin et al. 1995; Chapin and Shaver 1996). In boreal forests, fertilizing with N is well known to increase volume growth and tree foliage biomass (Axelsson and Axelsson 1986; Sigurdsson et al. 2013; Lim et al. 2015; From et al. 2016). Canopy closure occurring because of larger tree leaf area leads to reduced light availability for understory species. The C uptake of understory species can change because of this, and the direction of the change varies between species, as Palmroth et al. (2019) recently discovered in a Norway spruce site in northern Sweden. In their study, an increase in the leaf area index of trees together with annual N addition decreased the C uptake of bilberry and lingonberry, while the C uptake of wavy hair-grass increased. Despite the decrease in C uptake of the most dominating understory species, the contribution of the field layer to stand photosynthesis did not decrease. This was because the mean annual biomass of wavy hair-grass, which has a high photosynthetic capacity (Kulmala et al. 2009), increased to almost three-fold compared to the original situation, which was enough to keep field layer photosynthesis at its original level.

Canopy closure may protect the understory vegetation from heat, and the microclimate under the canopy may be a more important driver for understory species dynamics than the underlying macroclimate (Zellweger et al. 2020). This suggests that the common temperature data measured from the meteorological stations (at about a height of 2 m, relatively open surroundings) are not the best possible data to be used when modeling or predicting the effects of climate change on understory vegetation. In certain conditions, so-called microrefugia may form for sensitive plant species. Microrefugia are small areas where the microclimate creates such conditions that a species can survive despite general growing conditions becoming unfavorable for its persistence (Ashcroft et al. 2010; Keppel et al. 2012). Such microrefugia, or the effects of a microclimate, are relatively poorly known in the boreal region. However, the local microclimates may apparently even out the effect of a rising mean annual temperature on understory vegetation (Zellweger et al. 2020), and some plants at the edge of their range margins can persist in microrefugia when surrounding conditions change (Greiser et al. 2019).

As mentioned, climate change can cause similar changes as fertilization in the nutrient status of a northern ecosystem. Peñuelas et al. (2020) recently reported that the foliar nutrient contents of several tree species have decreased with increased atmospheric CO_2 concentrations in Europe during 1990–2016. This had occurred elsewhere, except in the north, where foliar N, sulfur, and calcium contents increased over time and P contents remained similar. The increased nutrient contents in the north correlated with increased mean annual temperature and the following enhanced availability of N in the soil. Annual precipitation sums also increased in the north during the study period, unlike in more southern locations, where increasingly dry conditions were considered to hinder nutrient uptake by plants.

In northern Finland, Rousi et al. (2017) found that increased N mineralization can be one of the main ways for the predicted northwards movement of the tree line. Their study implied that, contrary to previous beliefs, trees can move long distances towards the north if the climate warms and soil fertility is high. The species may also spread to regions where it previously did not grow (Rousi et al. 2017). Birch species together with Scots pine are expected to become more dominant and replace Norway spruce in many places (Kellomäki and Kolström 1992; Talkkari 1998; Kellomäki et al. 2001, 2005, 2008). Birch trees can be important for the nutrient circulation of a site (**I**), but also in other ways. For example, in northern Finland, mountain birch was able to facilitate Scots pine growth under its canopy despite the soil nutrient status (Mikola et al. 2018). Warmer temperatures may also cause changes in the elevational tree line, as Aakala et al. (2014) discovered in Värriö, where Scots pine has colonized on the tops of previously treeless fells during past decades. In addition to this newly organized distribution of an already existing species, new species may shift from more southern regions to the north. Plant species dynamics are very complex and many things can directly or indirectly alter species communities. For example, insect outbreaks are predicted to become more common with climate change. They can drastically decrease the photosynthetic rates of a forest, as observed in an outbreak of autumnal moth (*Epirrita autumnata*) and winter moth (*Operophtera brumata*) in a mountain birch site in northern Sweden (Olsson et al. 2017). In Finland, these particular species occur in the northernmost part of the country, but other insects may cause similar damage elsewhere.

5. CONCLUSIONS

Northern boreal forests are located at their growth limits, making them vulnerable to large-scale consequences of climate change, such as shifting of vegetation zones. On the other hand, these forests are considered relatively resilient, although the term resilience is somewhat hard to define and confusing to many (see e.g. Nikinmaa et al. 2020). Nevertheless, northern forests are expected to recover well after short disturbances such as extreme weather events. In this dissertation, I studied the baseline status and the responses of northern boreal forest vegetation to climate change. Several studies have shown the importance of the relationship of soil N and boreal vegetation cover. So far, soil P in boreal forests has received relatively little interest compared to N, and most studies regarding P have concentrated on former agricultural lands (Peltovuori 2007; Soinne et al. 2008) or on peatlands (e.g. Moilanen et al. 2010). However, an increasing number of studies imply that soil P is also important for northern forest vegetation growing on mineral soil. In our study (**I**), the N and P contents of the humus layer largely explained the understory community compositions in forests. Understory vegetation may have a substantial role in the carbon dynamics of a forest site, as was the case at the Värriö Scots pine site (**II**). Extreme weather events had occurred both at the Scots pine and Norway spruce sites and caused temporary changes in CO_2 flux rates (**III**). These changes occurred more clearly in the Norway spruce site.

The studied forest ecosystems seemed to be rather resilient to climatic extremes that have occurred at the sites so far (**III**), meaning that they recovered quickly and the vegetation was not physically damaged. If extreme weather events become stronger or more frequent, as predicted, the cold spells or droughts may cause severe damage to forest vegetation. Annual plants may die as a result, while perennial plants maybe survive but could lose some of their biomass. Droughts also increase the risk of fires, which greatly modify forest vegetation. A warmer temperature is predicted to increase the mineralization and availability of nutrients, but warm and dry conditions may also slow down organic matter decomposition in some forest sites, which seemed to be the case in Kenttärova spruce forest (**III**). The trees may photosynthesize more and begin growing better because of warmer temperatures, which is what our results also suggested (**II** and **III**). If this happens for a long enough period, the forests may begin resembling forests that grow in the central or southern boreal zones. Forest canopies may become more closed, which causes shading and changes in vegetation species, leading to changes in the carbon flux dynamics of these forests. Canopy closure will also increase interception, which means that in addition to decreased light levels the understory vegetation may end up with less water (Palmroth et al. 2019). The change in forest microclimate caused by increased shading may also protect the understory species from changes in the macroclimate such as rising air temperature (e.g. Zellweger et al. 2020).

Local variation in the nutrient availability of ecosystems may naturally also occur in the future. Possible mining-related changes may affect nutrient availability in the Värriö region. Open pit mining can lead to aerial deposition of phosphate and heavy metals, which in turn could change the nutrient dynamics and plant communities on a local scale. The region currently receives very little pollution, with air concentrations increasing only occasionally when the wind blows from the Kola Peninsula. Unlike soil N, P is not so dependent on climatic factors directly, but relies more on soil parent material and landforms (Augusto et al. 2017; Deiss et al. 2018). However, as the P cycle is connected with the N cycle, alterations in the N cycle due to climate change could impact the P cycle. This in turn can lead to changes in photosynthesis rates along with other carbon, energy, and water cycling between ecosystems and the atmosphere. The possible aerial deposition from the mine could speed up the otherwise slow movement of P in the ecosystems and affect nutrient cycles and vegetation compositions. It could have similar effects as e.g. the greater increased leaf litter input caused by increased shrub cover. The combined effects of mining and climate change are nevertheless hard to predict. The current processes, interactions, and feedbacks between soil nutrients, vegetation cover, and the atmosphere in northern boreal forest ecosystems require more research to be able to forecast the future changes. The role of the understory vegetation and its annual cycle, which differs from that of the forest canopy, is crucial in northern forest ecosystems in terms of carbon exchange. Yet, this is poorly considered in climate modeling because of the lack in research on the topic. Many research gaps also exist concerning how microclimates vs. macroclimates interact with species communities in northern latitudes. In addition to the scientific community, entities responsible for nature conservation, forest management, and other land use management would all benefit from filling these gaps in knowledge.

REFERENCES

Aakala T., Hari P., Dengel S., Newberry S. L., Mizunuma T., Grace J. (2014). A prominent stepwise advance of the tree line in north-east Finland. Journal of Ecology 102: 1582–1591. http://dx.doi.org/10.1111/1365-2745.12308

Aakala T., Berninger F., Starr M. (2018). The roles of competition and climate in tree growth variation in northern boreal old-growth forests. Journal of Vegetation Science 29: 1040–1051. https://doi.org/10.1111/jvs.12687

Aerts R., Chapin F.S. (1999). The mineral nutrition of wild plants revisited: A Re-evaluation of Processes and Patterns. Advances in Ecological Research 30: 1–67. https://doi-org.libproxy.helsinki.fi/10.1016/S0065-2504(08)60016-1

Akujärvi A., Hallikainen V., Hyppönen M., Mattila E., Mikkola K., Rautio P. (2014). Effects of reindeer grazing and forestry on ground lichens in Finnish Lapland. Silva Fennica 48 (3) article id 1153. 18 p. http://dx.doi.org/10.14214/sf.1153

Amthor J.S. (2000). The McCree-deWit-Penning de Vries-Thornley respiration paradigms: 30 years later. Annals of Botany 86: 1–20. https://doi.org/10.1006/anbo.2000.1175

Arnesen, G., Beck, P.S.A., Engelskjøn, T. (2007). Soil acidity, content of carbonates, and available phosphorus are the soil factors best correlated with Alpine vegetation: evidence from Troms, North Norway. Arctic, Antarctic and Alpine Research 39: 189–199. http://dx.doi.org/10.1657/1523-0430(2007)39[189:SACOCA]2.0.CO;2

Ashcroft M.B., Gollan J.R., Warton D.I., Ramp D. (2012). A novel approach to quantify and locate potential microrefugia using topoclimate, climate stability, and isolation from the matrix. Global Change Biology 18: 1866–1879. https://doi.org/10.1111/j.1365-2486.2012.02661.x

Augusto L., Achat D.L., Jonard M., Vidal D., Ringeval B. (2017). Soil parent material—A major driver of plant nutrient limitations in terrestrial ecosystems. Global Change Biology 23: 3808–3824. https://doi.org/10.1111/gcb.13691

Aurela M., Lohila A., Tuovinen J.-P, Hatakka J., Penttilä T., Laurila T. (2015). Carbon dioxide and energy flux measurements in four northern-boreal ecosystems at Pallas. Boreal Environment Research 20: 455–473. https://helda.helsinki.fi/handle/10138/228279. [Cited 7 April 2020].

Axelsson E., Axelsson B. (1986). Changes in carbon allocation patterns in spruce and pine trees following irrigation and fertilization. Tree Physiology 2: 189–204. https://doi.org/10.1093/treephys/2.1-2-3.189

Bakkenes M., Alkemade J.R.M., Ihle F., Leemans R., Latour J.B. (2002). Assessing effects of forecasted climate change on the diversity and distribution of European higher plants for 2050. Global Change Biology 8: 390–407. https://doi.org/10.1046/j.1354-1013.2001.00467.x

Baumgarten M., Hesse B.D., Augustaitienė I., Marozas V., Mozgeris G., Byčenkienė S., Mordas G., Pivoras A., Pivoras G., Juonytė D., Ulevičius V., Augustaitis A., Matyssek, R. (2019). Responses of species-specific sap flux, transpiration and water use efficiency of pine, spruce and birch trees to temporarily moderate dry periods in mixed forests at a dry and wet forest site in the hemi-boreal zone. Journal of Agricultural Meteorology 75: 13–29. https://doi.org/10.2480/agrmet.D-18-00008

Barber V.A., Juday G.P., Finney B.P. (2000). Reduced growth of Alaskan white spruce in the twentieth century from temperature-induced drought stress. Nature 405: 668–673. https://doi.org/10.1038/35015049

Beniston M. (2004). The 2003 heat wave in Europe: A shape of things to come? An analysis based on Swiss climatological data and model simulations. Geophysical Research Letters 31 https://doi.org/10.1029/2003GL018857

Bergeron O., Margolis H.A., Coursolle C. (2009). Forest floor carbon exchange of a boreal black spruce forest in eastern North America. Biogeosciences 6: 1849–1864. https://doi.org/10.5194/bg-6-1849-2009

Boisvenue C., Running S.W. (2006). Impacts of climate change on natural forest productivity – evidence since the middle of the 20th century. Global Change Biology 12: 862–882, doi:10.1111/j.1365-2486.2006.01134.x

Bret-Harte M.S., Shaver G.R., Zoerner J.P., Johnstone J.F., Wagner J.L., Chavez A.S., Gunkelman IV R.F., Lippert S.C., Laundre J.A. (2001). Developmental plasticity allows

Betula nana to dominate tundra subjected to an altered environment. Ecology 82: 18–32. https://doi.org/10.1890/0012-9658(2001)082[0018:DPABNT]2.0.CO;2

Brække F.H., Salih N. (2002). Reliability of Foliar Analyses of Norway Spruce Stands in a Nordic Gradient, Silva Fennica 36: 489–504, https://doi.org/10.14214/sf.540

Bäck J., Kolari P., Hari P. 2008. Respiration. Boreal Forest and Climate Change. pp. 176-180. Springer.

Cajander, A. K. (1909). Über Waldtypen. Acta Forestalia Fennica 1: 1–175.

Cajander, A. K. (1949). Forest types and their significance. Acta Forestalia Fennica 56: 1–71.

Ciais P., Reichstein M., Viovy N., Granier A., Ogée J., Allard V., Aubinet M., Buchmann N., Bernhofer C., Carrara A., Chevallier F., De Noble, N., Friend A.D., Friedlingstein P., Grünwald T., Heinesch B., Keronen P., Knohl A., Krinner G., Loustau D., Manca G., Matteucci G., Miglietta F., Ourcival J.M., Papale D., Pilegaard K., Rambal S., Seufert G., Soussana J.F., Sanz M.J., Schulze E.D., Vesala T., Valentini R. (2005). Europe-wide reduction in primary productivity caused by the heat and drought in 2003. Nature 437: 529–533. https://doi.org/10.1038/nature03972

Chapin III F.S., Shaver G.R., Giblin A.E., Nadelhoffer K.J., Laundre J.A. (1995). Responses of arctic tundra to experimental and observed changes in climate. Ecology 76: 694–711. http://dx.doi.org/10.2307/1939337

Chapin III F.S., Shaver G.R. (1996). Physiological and growth responses of arctic plants to a field experiment simulating climatic change. Ecology 77: 822–840. http://dx.doi.org/10.2307/2265504

Crowther T.W., Todd-Brown K.E.O., Rowe C.W., Wieder W.R., Carey J.C., Machmuller M.B., Snoek B.L., Fang S., Zhou G., Allison S.D., Blair J.M., Bridgham S.D., Burton A.J., Carrillo Y., Reich P.B., Clark J.S., Classen A.T., Dijkstra F.A., Elberling B., Emmett B.A., Estiarte M., Frey S.D., Guo J., Harte J., Jiang L., Johnson B.R., Kröel-Dulay G., Larsen K.S., Laudon H., Lavallee J.M., Luo Y., Lupascu M., Ma L.N., Marhan S., Michelsen A., Mohan J., Niu S., Pendall E., Peñuelas J., Pfeifer-Meister L., Poll C., Reinsch S., Reynolds L.L., Schmidt I.K., Sistla S., Sokol N.W., Templer P.H., Treseder K.K., Welker J.M., Bradford M.A. (2016). Quantifying global soil carbon losses in response to warming. Nature 540: 104–108. https://doi.org/10.1038/nature20150

Davidson E., Janssens I. (2006). Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440: 165–173. https://doi.org/10.1038/nature04514

Dirnböck T., Grandin U., Bernhardt-Römermann M., Beudert B., Canullo R., Forsius M., Grabner M.-T., Holmberg M., Kleemola S., Lundin L., Mirtl M., Neumann M., Pompei E., Salemaa M., Starlinger F., Staszewski T., Uzieblo A.K. (2014). Forest floor vegetation response to nitrogen deposition in Europe, Global Change Biology 20: 429–440. https://doi.org/10.1111/gcb.12440

Deiss L., de Moraes B.A., Maire V. (2018). Environmental drivers of soil phosphorus compositionin natural ecosystems. Biogeosciences 15: 4575–4592. https://doi.org/10.5194/bg-15-4575-2018

DeLucia E.H., Drake J.E., Thomas R.B., Gonzalez-Meler M. (2007). Forest carbon use efficiency: is respiration a constant fraction of gross primary production? Global Change Biology 13: 1157–1167. https://doi.org/10.1111/j.1365-2486.2007.01365.x

Dormann, C.F., Woodin S.J. (2002). Climate change in the Arctic: using plant functional types in a meta-analysis of field experiments. Functional Ecology 16: 4–17. https://doi.org/10.1046/j.0269-8463.2001.00596.x

Dupré C., Wessberg C., Diekmann M. (2002) Species richness in deciduous forests: Effects of species pools and environmental variables, Journal of Vegetation Science 13: 505–516. https://doi.org/10.1111/j.16541103.2002.tb02077.x

Eilmann B., Rigling A. (2012). Tree-growth analyses to estimate tree species’ drought tolerance. Tree Physiology 32: 178–187. https://doi.org/10.1093/treephys/tps004

FAO: FAO/Unesco Soil map of the world, revised legend, World Soil Resources Report 60, FAO, Rome, 140 pp., 1988.

From F., Lundmark T., Mörling T., Pommerening A., Nordin A. (2016). Effects of simulated long-term N deposition on Picea abies and Pinus sylvestris growth in boreal forest. Canadian Journal of Forest Research 46: 1396–1403. https://dx.doi.org/10.1139/cjfr-2016-0201

Ganthaler A., Mayr S. (2015). Dwarf shrub hydraulics: two Vaccinium species (Vaccinium myrtillus, Vaccinium vitis-idaea) of the European Alps compared. Physiologia Plantarum 155: 424–434. https://doi.org/10.1111/ppl.12333

Gao Y., Markkanen T., Thum T., Aurela M., Lohila A., Mammarella I., Kämäräinen M., Hagemann S., Aalto T. (2016). Assessing various drought indicators in representing summer drought in boreal forests in Finland, Hydrology and Earth System Sciences 20: 175–191. https://doi.org/10.5194/hess-20-175-2016

Gao Y., Markkanen T., Thum T., Aurela M., Mammarella I., Thum T., Tsuruta A., Yang H., Aalto T. (2017). Response of water use efficiency to summer drought in a boreal Scots pine forest in Finland. Biogeosciences 14: 4409–4422. https://doi.org/10.5194/bg-14-4409-2017

Greiser C., Ehrlén J., Meineri E., Hylander K. (2019). Hiding from the climate: Characterizing microrefugia for boreal forest understory species. Global Change Biology 26: 471–483. https://doi.org/10.1111/gcb.14874

Gu L., Hanson P.J., Post W.M., Kaiser D.P., Yang B., Nemani R., Pallardy S.G., Meyers T. (2008). The 2007 Eastern US Spring Freeze: Increased Cold Damage in a Warming World? Bioscience 58: 253–262. https://doi.org/10.1641/B580311

Gundale M.J., From F., Bach L.H., Nordin A. (2014). Anthropogenic nitrogen deposition in boreal forests has a minor impact on the global carbon cycle. Global Change Biology 20: 276–286. https://doi.org/10.1111/gcb.12422

Gutschick V.P., BassiriRad H. (2003). Extreme events as shaping physiology, ecology, and evolution of plants: toward a unified definition and evaluation of their consequences. New Phytologist 160: 21–42. https://doi.org/10.1046/j.1469-8137.2003.00866.x

Hari P., Vesala T., Kolari P., Launiainen S., Rannik Ü., Kulmala L., Kabiri Koupaei K., Nikinmaa E. (2013). CO2, Water Vapour and Energy Fluxes Between Forest Ecosystem and Atmosphere. In Hari P., Heliövaara K. and Kulmala L. (eds). Physical and Physiological Forest Ecology. pp. 75-101. Springer.

Hari P., Mäkelä A. (2003). Annual pattern of photosynthesis in Scots pine in the boreal zone. Tree Physiology 23: 145–155. https://doi.org/10.1093/treephys/23.3.145

Harte J., Shaw R. (1995). Shifting dominance within a montane vegetation community: results of a climate-warming experiment. Science 267: 876–880. https://doi.org/10.1126/science.267.5199.876

Hartmann D.L., Klein Tank A.M.G., Rusticucci M., Alexander L.V., Brönnimann S., Charabi Y., Dentener F.J., Dlugokencky E.J., Easterling D.R., Kaplan A., Soden B.J., Thorne P.W., Wild M. and Zhai P.M., (IPCC) 2013: Observations: Atmosphere and Surface. In: Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Stocker, T.F., Qin D., Plattner G.-K., Tignor M., Allen S.K., Boschung J., Nauels A., Xia Y., Bex V. and Midgley P.M. (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Havström M., Callaghan T.V., Jonasson S. (1993). Differential growth responses of Cassiope tetragona, an arctic dwarf-shrub, to environmental perturbations among three contrasting high- and subarctic sites. Oikos 66: 389–402. https://doi.org/10.2307/3544933

Hedwall P.-O., Bergh J., Brunet J. (2017). Phosphorus and nitrogen co-limitation of forest ground vegetation under elevated anthropogenic nitrogen deposition. Oecologia 185: 317–326. https://doi.org/10.1007/s00442-017-3945-x

Hicks Pries C.E., Schuur E.A.G., Vogel J.G., Natali S.M. (2013). Moisture drives surface decomposition in thawing tundra. Journal of Geophysical Research: Biogeosciences 118: 1133–1143. http://dx.doi.org/10.1002/jgrg.20089

Hinsinger P. (2001). Bioavailability of soil inorganic P in the rhizosphere as affected by root-induced chemical changes: a review. Plant and Soil 237: 173–195. http://dx.doi.org/10.1023/A:1013351617532

Hobbie S.E., Chapin III F.S. (1998). The response of tundra plant biomass, aboveground production, nitrogen, and CO2 flux to experimental warming. Ecology 79: 1526–1544. https://doi.org/10.2307/176774

Hobbie S.E., Nadelhoffer K.J., Högberg P. (2002). A synthesis: The role of nutrients as constraints on carbon balances in boreal and arctic regions. Plant and Soil 242: 163–170. http://dx.doi.org/10.1023/A:1019670731128

Hobbie S.E., Gough L. (2002). Foliar and soil nutrients in tundra on glacial landscapes of contrasting ages in northern Alaska. Oecologia 131:253–462. https://doi.org/10.1007/s00442-002-0892-x

Hotanen J.-P., Nousiainen H., Mäkipää R., Reinikainen A., Tonteri T. (2008). Metsätyypit - opas kasvupaikkojen luokitteluun. Metsäkustannus. 192 s.

Hämet-Ahti L., 1981. The boreal zone and its biotic subdivision. Fennia 159 : 69-75.

Ikawa H., Nakai T., Busey R.C., Kim Y., Kobayashi H., Nagai S., Ueyama M., Saito K., Nagano H., Suzuki R., Hinzman L. (2015). Understory CO2, sensible heat, and latent heat fluxes in a black spruce forest in interior Alaska. Agricultural and Forest Meteorology 214: 80–90. https://doi.org/10.1016/j.agrformet.2015.08.247

Ilvesniemi H., Levula J., Ojansuu R., Kolari P., Kulmala L., Pumpanen J., Launiainen S., Vesala T., Nikinmaa E. (2009). Long-term measurements of the carbon balance of a boreal Scots pine dominated forest ecosystem. Boreal Environment Research 14: 731–753. https://helda.helsinki.fi/handle/10138/233557. [Cited 18 May 2020]

Jonasson S., Michelsen A., Schmidt I.K., Nielsen E.V. (1999). Responses in microbes and plants to changed temperature, nutrient, and light regimes in the Arctic. Ecology 80: 1828–1843. https://doi.org/10.1890/0012-9658(1999)080[1828:RIMAPT]2.0.CO;2

Jones M.H., Fahnestock J.T., Walker D.A., Walker M.D., Welker J.M. (1998). Carbon dioxide fluxes in moist and dry arctic tundra during season: Responses to increases in summer temperature and winter snow accumulation. Arctic and Alpine Research 30: 373–380. https://doi.org/10.2307/1552009

Jónsdóttir I.S., Magnússon B., Gudmundsson J., Elmarsdóttir A., Hjartarson H. (2005). Variable sensitivity of plant communities in Iceland to experimental warming. Global Change Biology 11: 553–563. https://doi.org/10.1111/j.1365-2486.2005.00928.x

Kalliokoski T., Aalto T., Bäck J., Ezhova E., Franz D., Haapanala S., Juurola E., Kerminen V.-M., Kolari P., Kulmala L., Liski J., Mammarella I., Matkala L., Petäjä T., Rantala P., Vesala T., Kulmala M. (2019). Carbon sink and CarbonSink+: from observations to global potential. University of Helsinki. https://helda.helsinki.fi//bitstream/handle/10138/312250/Carbon_sink_and_CarbonSink_from_observations_to_global_potential_12062019.pdf?sequence=1 [Cited 27 May 2020].

Kersalo J., Pirinen P. (2009). Suomen maakuntien ilmasto (The climate of Finnish regions). Reports 2009:8, Finnish Meteorological Institute. Yliopistopaino, Helsinki, Finland, 196 pp.

Kellomäki S., Kolström M. (1992). Simulation of tree species composition and organic matter accumulation in Finnish boreal forests under changing climatic conditions. Vegetatio 102:47–68. www.jstor.org/stable/20046200. [Cited 30 April 2020]

Kellomäki S., Rouvinen I., Peltola H., Strandman H., Steinbrecher R. (2001). Impact of global warming on the tree species composition of boreal forests in Finland and effects on emissions of isoprenoids. Global Change Biology 7:531–544. https://doi.org/10.1046/j.1365-2486.2001.00414.x

Kellomäki S., Strandman H., Nuutinen T., Peltola H., Korhonen K. T., Väisänen H. (2005). Adaptation of forest ecosystems, forests and forestry to climate change. FINADAPT Working Paper 4, Finnish Environment Institute Mimeographs 334, Helsinki, 44 pp.

Kellomäki S., Peltola H., Nuutinen T., Korhonen K.T., Strandman H. (2008). Sensitivity of managed boreal forests in Finland to climate change, with implications for adaptive management. Philosophical transactions of the Royal Society of London. Series B, Biological sciences 363: 2339–2349. https://doi.org/10.1098/rstb.2007.2204

Keppel G., Van Niel K.P., Wardell-Johnson G.W., Yates C.J., Byrne M., Mucina L., Schut A.G.T., Hopper S.D., Franklin S.E. (2012). Refugia: Identifying and understanding safe havens for biodiversity under climate change. Global Ecology and Biogeography 21: 393–404. https://doi.org/10.1111/j.1466-8238.2011.00686.x

Kielland K., McFarland J.W., Ruess R.W., Olson K. (2007). Rapid cycling of organic nitrogen in taiga forest ecosystems. Ecosystems 10: 360–368. https://doi.org/10.1007/s10021-007-9037-8

Koerselman W., Meuleman A.F.M. (1996). The vegetation N : P ratio: a new tool to detect the nature of nutrient limitation. Journal of Applied Ecology 33: 1441–1450. https://doi.org/10.2307/2404783

Kolari P., Pumpanen J., Kulmala L., Ilvesniemi H., Nikinmaa E., Gronholm T., Hari P. (2006). Forest floor vegetation plays an important role in photosynthetic production of boreal forests. Forest Ecology and Management 221: 241–248. https://doi.org/10.1016/j.foreco.2005.10.021

Kolari P., Lappalainen H.K., Hänninen H., Hari P. (2007). Relationship between temperature and the seasonal course of photosynthesis in Scots pine at northern timberline and in southern boreal zone. Tellus B: Chemical and Physical Meteorology 59: 542–552. https://doi.org/10.1111/j.1600-0889.2007.00262.x

Korhonen J.F.J., Pihlatie M., Pumpanen J., Aaltonen H., Hari P., Levula J., Kieloaho A.-J., Nikinmaa E., Vesala T., Ilvesniemi H. (2013). Nitrogen balance of a boreal Scots pine forest. Biogeosciences 10: 1083–1095. https://doi.org/10.5194/bg-10-1083-2013

Kreutz A., Aakala T., Grenfell R., Kuuluvainen T. (2015). Spatial tree community structure in three stands across a forest succession gradient in northern boreal Fennoscandia. Silva Fennica vol. 49 no. 2 article id 1279. 17 p.

Kulmala L., Pumpanen J., Vesala T., Hari P. (2009). Photosynthesis of boreal ground vegetation after a forest clear-cut. Biogeosciences 6: 2495–2507. https://doi.org/10.5194/bg-6-2495-2009

Kulmala L, Pumpanen J, Kolari P, Muukkonen P, Hari P, Vesala T (2011). Photosynthetic production of ground vegetation in different-aged Scots pine (Pinus sylvestris) forests. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 41: 2020-2030. https://doi.org/10.1139/X11-121

Kurz W.A., Stinson G., Rampley G. (2008). Could increased boreal forest ecosystem productivity offset carbon losses from increased disturbances? Philosophical Transactions: Biological Sciences 363: 2259–2268. https://doi.org/10.1098/rstb.2007.2198

Kyrö E.-M., Väänänen R., Kerminen V.-M., Virkkula A., Petäjä T., Asmi A., Dal Maso M., Nieminen T., Juhola S., Shcherbinin A., Riipinen I., Lehtipalo K., Keronen P., Aalto P. P., Hari P., Kulmala M. (2014). Trends in new particle formation in eastern Lapland, Finland: effect of decreasing sulfur emissions from Kola Peninsula. Atmospheric Chemistry and Physics 14: 4383–4396. https://doi.org/10.5194/acp-14-4383-2014

Körner C. (2003). Carbon limitation in trees. Journal of Ecology 91: 4–17. https://doi.org/10.1046/j.1365-2745.2003.00742.x

Köster K., Berninger F., Lindén A., Köster E., Pumpanen J. (2014). Recovery in fungal biomass is related to decrease in soil organic matter turnover time in a boreal fire chronosequence. Geoderma 235–236: 74–82. https://doi.org/10.1016/j.geoderma.2014.07.001

Law B., Falge E., Gu L., Baldocchi D., Bakwin P., Berbigier P., Davis K., Dolman A., Falk M., Fuentes J., Goldstein A., Granier A., Grelle A., Hollinger D., Janssens I., Jarvis P., Jensen N., Katul G., Mahli Y., Matteucci G., Meyers T., Monson R., Munger W., Oechel W., Olson R., Pilegaard K., Paw K., Thorgeirsson H., Valentini R., Verma S., Vesala T., Wilson K., Wofsy S. (2002). Environmental controls over carbon dioxide and water vapor exchange of terrestrial vegetation. Agricultural and Forest Meteorology 113: 97–120. https://doi.org/10.1016/S0168-1923(02)00104-1

Lebourgeois F., Rathgebe C.B.K., Ulrich E. (2010). Sensitivity of French temperate coniferous forests to climate variability and extreme events (Abies alba, Picea abies and Pinus sylvestris). Journal of Vegetation Science 21: 364–376. https://doi.org/10.1111/j.1654-1103.2009.01148.x

Lebourgeois F., Merian P., Courdier F., Ladier J., Dreyfus P. (2012). Instability of climate signal in tree-ring width in Mediterranean mountains: a multi-species analysis. Trees 26: 715–729. https://doi.org/10.1007/s00468-011-0638-7

Lévesque M., Saurer M., Siegwolf R., Eilmann B., Brang P., Bugmann H., Rigling A. (2013). Drought response of five conifer species under contrasting water availability suggests high vulnerability of Norway spruce and European larch. Global Change Biology 19: 3184–3199. https://doi.org/10.1111/gcb.12268

Lindner M., Maroschek M., Netherer S., Kremer A., Barbati A., Garcia-Gonzalo J., Seidl R., Delzon S., Corona P., Kolström M., Lexer M.J., Marchetti M. (2010). Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. Forest Ecology and Management 259:698–709. https://doi.org/10.1016/j.foreco.2009.09.023

Linkosalmi M., Aurela M., Tuovinen J.-P., Peltoniemi M., Tanis C.M., Arslan A.N., Kolari P., Böttcher K., Aalto T., Rainne J., Hatakka J., Laurila T. (2016). Digital photography for assessing the link between vegetation phenology and CO2 exchange in two contrasting northern ecosystems. Geoscientific Instrumentation, Methods and Data Systems 5: 417–426. https://doi.org/10.5194/gi-5-417-2016

Linkosalo T., Heikkinen J., Pulkkinen P., Mäkipää R. (2014). Fluorescence measurements show stronger cold inhibition of photosynthetic light reactions in Scots pine compared to

Norway spruce as well as during spring compared to autumn. Frontiers in Plant Science 5: 1–8. https://doi.org/10.3389/fpls.2014.00264.

Lim H., Oren R., Palmroth S., Torngern P., Morling T., Nasholm T., Lundmark T., Helmisaari H.S., Leppälammi-Kujansuu J., Linder S. (2015). Inter-annual variability of precipitation constrains the production response of boreal Pinus sylvestris to nitrogen fertilization. Forest Ecology and Management 348: 31–45. https://doi.org/10.1016/j.foreco.2015.03.029

Liski J. (1995). Variation in soil organic carbon and thickness of soil horizons within a boreal forest stand – effect of trees and implications for sampling. Silva Fennica 29: 255–266, https://doi.org/10.14214/sf.a9212

Lladó S., López-Mondéjar R., Baldrian P. (2017). Forest Soil Bacteria: Diversity, Involvement in Ecosystem Processes, and Response to Global Change. Microbiology and Molecular Biology Reviews 81: 27 pp https://doi.org/10.1128/MMBR.00063-16

Lundmark T., Hällgren J. (1987). Effect of frost on shaded and exposed spruce and pine seedlings planted in the field. Canadian Journal of Forest Research 17: 1197–1201. https://doi.org/10.1139/x87-184

Marschner H. (1995). Mineral Nutrition of Higher Plants, Academic Press Limited, Cambridge, Great Britain, 889 pp.

Merilä P., Derome J. (2008): Relationships between needle nutrient composition in Scots pine and Norway spruce stands and the respective concentrations in the organic layer and in percolation water. Boreal Environment Research 13: 35–47. https://jukuri.luke.fi/handle/10024/514721 [Cited 18 May 2020]

Mikola J., Silfver T., Rousi M. (2018). Mountain birch facilitates Scots pine in the northern tree line –does improved soil fertility have a role? Plant and Soil 423:205–213. https://doi.org/10.1007/s11104-017-3517-1

Minchin, P.R. (1987). An evaluation of the relative robustness of techniques for ecological ordination. Vegetatio 69: 89–107. https://doi.org/10.1007/BF00038690

Moilanen M., Saarinen M., Silfverberg K. (2010). Foliar nitrogen, phosphorus and potassium concentrations of Scots pine in drained mires in Finland. Silva Fennica 44: 583–601. https://doi.org/10.14214/sf.129

Moyano E., Manzoni S., Chenu C. (2013). Responses of soil heterotrophic respiration to moisture availability: An exploration of processes and models. Soil Biology and Biochemistry 59: 72–85. https://doi.org/10.1016/j.soilbio.2013.01.002.

Mäkelä A., Kolari P., Karimaki J., Nikinmaa E., Perämäki M., Hari P. (2006). Modelling five years of weather-driven variation of GPP in a boreal forest. Agricultural and Forest Meteorology 139: 382–398. https://doi.org/10.1016/j.agrformet.2006.08.017

Mäkelä A., Pulkkinen M., Kolari P., Lagergren F., Berbigier P., Lindroth A., Loustau D., Nikinmaa E., Vesala T., Hari P. (2008). Developing an empirical model of stand GPP with the LUE approach: analysis of eddy covariance data at five contrasting conifer sites in Europe. Global Change Biology 14: 92–108. https://doi.org/10.1111/j.1365-2486.2007.01463.x

Mäkipää R. (1999). Response Patterns of Vaccinium myrtillus and V. vitis-idaea along Nutrient Gradients in Boreal Forest, Journal of Vegetation Science 10: 17–26. https://doi.org/10.2307/3237156

Nemani R.R., Keeling C.D., Hashimoto H., Jolly W.M., Piper S.C., Tucker C.J., Myneni R.B., Running S.W. (2003). Climate-Driven Increases in Global Terrestrial Net Primary Production from 1982 to 1999. Science 300: 1560–1563. https://doi.org/10.1126/science.1082750

Nikinmaa L., Lindner M, Cantarello E., Jump A. S., Seidl R., Winkel G., Muys B. (2020). Reviewing the use of resilience concepts in forest sciences. Current Forestry Reports https://doi.org/10.1007/s40725-020-00110-x

Näsholm T., Kielland K., Ganeteg U. (2008). Uptake of organic nitrogen by plants. New Phytologist 182: 31–48. https://doi.org/10.1111/j.1469-8137.2008.02751.x

Paatero J., Dauvalter V., Derome J., Lehto J., Pasanen J., Vesala T., Miettinen J., Makkonen U., Kyrö E.-M., Jernström J.,Isaeva L., Derome K. (2008). Effects of Kola air pollution on the environment in the western part of the Kola peninsula and Finnish Lapland: final report. Finnish Meteorological Institute Reports 6: 1–26. https://helda.helsinki.fi/handle/10138/1202 [Cited 19 May 2020]

Palmroth S., Bach L.H., Lind M., Kolari P., Nordin A., Palmqvist K. (2019). Nitrogen supply and other controls of carbon uptake of understory vegetation in a boreal Picea abies forest. Agricultural and Forest Meteorology 276–277: 1–11. https://doi.org/10.1016/j.agrformet.2019.107620

Pan Y., Birdsey R.A., Fang J., Houghton R., Kauppi P.E., Kurz W.A., Phillips O.L., Shivdenko A., Lewis S.L., Canadell J.G., Ciais P., Jackson R.B., Pacala S.W., McGuire D., Piao S., Rautianen A., Sitch S., Hayes D. (2011). A Large and Persistent Carbon Sink in the World’s Forests. Science 333: 988-993. https://doi.org/10.1126/science.1201609

Park T., Sangram G., Tømmervik H., Euskirchen E.S., Høgda K.-A., Karlsen S.R., Brovkin V., Nemani R.R., Myneni R.B. (2016). Changes in growing season duration and productivity of northern vegetation inferred from long-term remote sensing data. Environmental Research Letters 11: 1–11. https://doi.org/10.1088/1748-9326/11/8/084001

Peltovuori T. (2007). Sorption of phosphorus in field-moist and air-dried samples from four weakly developed cultivated soil profiles. European Journal of Soil Science 58: 8–17. http://dx.doi.org/10.1111/j.1365-2389.2006.00789.x

Peñuelas J., Fernández-Martínez M., Vallicrosa H., Maspons J., Zuccarini P., Carnicer J., Sanders T.G.M., Krüger I., Obersteiner M., Janssens I.A., Ciais P., Sardans J. (2020). Increasing atmospheric CO concentrations correlate with declining nutritional status of European forests. Communications biology 3: 1–25. https://doi.org/10.1038/s42003-020-0839-y

Pirinen P., Simola H., Aalto J., Kaukoranta J.-P., Karlsson P., Ruuhela R. (2012). Tilastoja Suomen ilmastosta 1981–2010, Ilmatieteen laitos, Raportteja 2012:1, Finnish Meteorological Institute, 94 pp. https://helda.helsinki.fi/handle/10138/35880 [Cited 19 May 2020]

Pöyry Environment (2009). Soklin kaivoshankkeen YVA-selostus, 332 pp.

R Development Core Team (2017). R: A Language and Environment forStatistical Computing, R Foundation for Statistical Computing. http://www.R-project.org/ [Cited 19 May 2020]

Raghothama K. G. (1999). Phosphate acquisition. Annual Review of Plant Physiology and Plant Molecular Biology 50: 665–93. http://dx.doi.org/10.1146/annurev.arplant.50.1.665

Reinikainen A., Mäkipää R., Vanha-Majamaa I., Hotanen J.-P. (2000). Kasvit muuttuvassa metsäluonnossa (Changes in the frequency and abundances of forest and mire plants in Finland since 1950). Kustannusyhtiö Tammi, Helsinki

Reta G., Dong X., Li Z., Su B., Hu X., Bo H., Yu D., Wan H., Liu J., Li Y., Xu G., Wang K., Xu S. (2018). Environmental impact of phosphate mining and beneficiation: review. Internationa Journal of Hydrology 2: 424–431. https://doi.org/10.15406/ijh.2018.02.00106

Rinnan R., Michelsen A., Jonasson S. (2008). Effects of litter addition and warming on soil carbon, nutrient pools and microbial communities in a subarctic heath ecosystem. Applied Soil Ecology 39: 271–281. https://doi.org/10.1016/j.apsoil.2007.12.014

Robinson C.H. (2002). Controls on decomposition and soil nitrogen availability at high latitudes. Plant and Soil 242: 65–81. http://dx.doi.org/10.1023/A:1019681606112

Rousi M., Possen B.J.M.H., Ruotsalainen S., Silfver T., Mikola J. (2017). Temperature and soil fertility as regulators of tree line Scots pine growth and survival—implications for the acclimation capacity of northern populations. Global change biology 24: 545–559. https://doi.org/10.1111/gcb.13956

Ruosteenoja K., Markkanen T., Venäläinen A., Räisänen P., Peltola H. (2017). Seasonal soil moisture and drought occurrence in Europe in CMIP5 projections for the 21st century. Climate Dynamics 50: 1177–1192. https://doi.org/10.1007/s00382-017-3671-4

Rustad L.E., Campbell J.L., Marion G.M., Norby R.J., Mitchell M.J., Hartley A.E., Cornelissen J.H.C., Gurevitch J., GCTE-NEWS (2001). A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. Oecologia 126: 543–562. http://dx.doi.org/10.1007/s004420000544

Ruuskanen T.M., Reissel A., Keronen P., Aalto P.P., Laakso L., Grönholm T., Hari P., Kulmala M. (2003). Atmospheric trace gas and aerosol particle concentration measurements in Eastern Lapland, Finland 1992-2001. Boreal Environment Research 8: 335–349. http://www.borenv.net/BER/pdfs/ber8/ber8-335.pdf [Cited 19 May 2020]

Ryan M.G. (1991). Effects of Climate Change on Plant Respiration. Ecological Applications 1: 157–167. https://doi.org/10.2307/1941808

Saarsalmi A., Mälkönen E. (2001). Forest Fertilization Research in Finland: A Literature Review. Scandinavian Journal of Forest Research 16: 514–535. https://doi.org/10.1080/02827580152699358

Sætersdal M., Birks H.J.B., Peglar S.M. (1998). Predicting changes in Fennoscandian vascular plant species richness as a result of future climatic change. Journal of Biogeography 25: 111–122. https://doi.org/10.1046/j.1365-2699.1998.251192.x

Salemaa M., Derome J., Nöjd P. (2008). Response of boreal forest vegetation to the fertility status of the organic layer along a climatic gradient. Boreal Environment Research 13: 48–66. https://helda.helsinki.fi/handle/10138/235262 [Cited 19 May 2020]

Seastedt T.R, Vaccaro L. (2001). Plant species richness, productivity, and nitrogen and phosphorus limitations across a snowpack gradient in alpine tundra, Colorado, U.S.A. Arctic, Antarctic and Alpine Research 33:100–106. https://doi.org/10.2307/1552283

Seneviratne S.I., Nicholls N., Easterling D., Goodess C.M., Kanae S., Kossin J., Luo Y., Marengo J., McInnes K., Rahimi M., Reichstein M., Sorteberg A., Vera C., Zhang X. (2012). Changes in climate extremes and their impacts on the natural physical environment. In: Managing the Risks of Extreme Events and Disasters to Advance Climate Change Adaptation [Field C.B., Barros V., Stocker T.F., Qin D., Dokken D.J., Ebi K.L., Mastrandrea M.D., Mach K.J., Plattner G.-K., Allen S.K., Tignor M., Midgley P.M. (eds.)]. A Special Report of Working Groups I and II of the Intergovernmental Panel on ClimateChange (IPCC). Cambridge University Press, Cambridge, UK, and New York, NY, USA, pp. 109-230

Serreze M.C., Barry R.G. (2011). Processes and impacts of Arctic amplification: A research synthesis. Global and Planetary Change 77: 85–96. doi:10.1016/j.gloplacha.2011.03.004

Sierra C.A., Trumbore S.E., Davidson E.A., Vicca S., Janssens I. (2015). Sensitivity of decomposition rates of soil organic matter with respect to simultaneous changes in temperature and moisture. Journal of Advances in Modeling Earth Systems 7: 335–356 https://doi.org/10.1002/2014MS000358.

Sigurdsson B.D., Medhurst J., Wallin G., Eggertsson O., Linder S. (2013). Growth of mature boreal Norway spruce was not affected by elevated [CO2] and/or air temperature unless nutrient availability was improved. Tree Physiology 33: 1192–1205. https://doi.org/10.1093/treephys/tpt043

Shaver G.R., Johnson L.C., Cades D.H., Murray G., Laundre J.A., Rastetter E.B., Nadelhoffer K.J., Giblin A.E. (1998). Biomass and CO2 flux in wet sedge tundras: Responses to nutrients, temperature and light. Ecological Monographs 68: 75–97. http://dx.doi.org/10.1890/0012-9615(1998)068[0075:BACFIW]2.0.CO;2

Shaver G.R., Chapin III F.S. (1995). Long-term responses to factorial, NPK fertilizer treatment by Alaskan wet and moist tundra sedge species. Ecography 18: 259–275. www.jstor.org/stable/3682807 [Cited 7 May 2020]

Skov F., Svenning J.-C. (2004). Potential impact of climatic change on the distribution of forest herbs in Europe. Ecography 27: 366–380. https://doi.org/10.1111/j.0906-7590.2004.03823.x

Smith M.D. (2011). An ecological perspective on extreme climatic events: a synthetic definition and framework to guide future research. Journal of Ecology 99: 656–663. https://doi.org/10.1111/j.1365-2745.2011.01798.x

Soinne H., Saarijärvi K., Karppinen M., Hartikainen H. (2008). Sensitivity of soil phosphorus tests in predicting the potential risk of phosphorus loss from pasture soil. Agricultural and Food Science 17: 265– 277. https://doi.org/10.2137/145960608786118785

Sorensen P.L., Michelsen A. (2011). Long-term warming and litter addition affects nitrogen fixation in a subarctic heath. Global Change Biology 17: 528–537. https://doi.org/10.1111/j.1365-2486.2010.02234.x

Soudzilovskaia N.A., Onipchenko V.G., Cornelissen J.H.C., Aerts R. (2005). Biomass production, N:P ratio and nutrient limitation in a Caucasian alpine tundra plant community. Journal of Vegetation Science 16: 399–406. https://doi.org/10.1111/j.1654-1103.2005.tb02379.x

Stark S. (2007) Nutrient cycling in the tundra. In: Marschner P., Rengel Z. (eds) Nutrient cycling in terrestrial ecosystems. Springer, Berlin

Strengbom J., Nordin A., Näsholm T., Ericson L. (2002). Parasitic fungus mediates vegetational changes in nitrogen exposed boreal forest. Journal of Ecology 90: 61–67. https://doi.org/10.1046/j.0022-0477.2001.00629.x

Sturm M., Racine C., Tape K. (2001). Increasing shrub abundance in the Arctic. Nature 411: 546-547. https://doi.org/10.1038/35079180

Susiluoto S., Rasilo T., Pumpanen J., Berninger F., 2008. Effects of grazing on the vegetation structure and carbon dioxide exchange of a Fennoscandian fell ecosystem. Arctic, Antarctic, and Alpine Research 40: 422–431. http://dx.doi.org/10.1657/1523-0430(07-035)[SUSILUOTO]2.0.CO;2

Swanson R.V., Flanagan L.B. (2001). Environmental regulation of carbon dioxide exchange at the forest floor in a boreal black spruce ecosystem. Agricultural and Forest Meteorology 108: 165–181. https://doi.org/10.1016/S0168-1923(01)00243-X

Sykes M.T., Prentice I.C., Cramer W. (1996). A bioclimatic model for the potential distributions of north European tree species under present and future climates. Journal of Biogeography 23: 203–233.

Sjögersten S., Wookey P. (2004). Decomposition of mountain birch leaf litter at the forest-tundra ecotone in the Fennoscandian mountains in relation to climate and soil conditions. Plant and Soil 262: 215–227. https://doi.org/10.1023/B:PLSO.0000037044.63113.fe

Talkkari A. (1998). The development of forest resources and potential wood yield in Finland under changing climatic conditions. Forest Ecology and Management 106: 97–106. https://doi.org/10.1016/S0378-1127(97)00300-9

Tamm C.O. (1991). Nitrogen in terrestrial ecosystems: Questions of productivity, vegetational changes, and ecosystem stability, Ecological Studies 81, Spriger-Verlag, Berlin, Heidelberg, 116 pp.

Thuiller W. 2003. BIOMOD – optimizing predictions of species distributions and projecting potential future shifts under global change. Global Change Biology 9: 1353-1362. https://doi.org/10.1046/j.1365-2486.2003.00666.x

Tikkanen E. (editor) (1995). Kuolan saastepäästöt Lapin metsien rasitteena. Itä-Lapin metsävaurioprojektin loppuraportti. Maa- ja metsätalousministeriö, Metsäntutkimuslaitos. Gummerrus kirjapaino Jyväskylä. 232 pp.

Vadeboncoeur M.A. (2010). Meta-analysis of fertilization experiments indicates multiple limiting nutrients in northeastern deciduous forests. Canadian Journal of Forest Research 40: 1766–1780. http://dx.doi.org/10.1139/X10-127

Vance C.P., Uhde-Stone C., Allan D.L. (2003). Phosphorus acquisition and use: critical adaptations by plants for securing a nonrenewable resource. New Phytologist 157: 423-447. http://dx.doi.org/10.1046/j.1469-8137.2003.00695.x

Vartiainen H., Paarma, H. (1979). Geological Characteristics of the Sokli Carbonatite Complex, Finland. Economic Geology and the Bulletin of the Society of Economic Geologists 74: 1296–1306.

van der Maaten-Theunissen M., Kahle H.-P., Maaten E. (2013). Drought sensitivity of Norway spruce is higher than that of silver fir along an altitudinal gradient in southwestern Germany. Annals of Forest Science 70: 185–193. https://doi.org/10.1007/s13595-012-0241-0

van Wijk M.T., Clemmensen K.E., Shaver G.R., Williams M., Callaghan T.V, Chapin III F.S., Cornelissen J.H.C., Gough L., Hobbie S.E., Jonasson S., Lee J.A., Michelsen A., Press M.C., Richardson S.J., Rueth H. (2003). Long-term ecosystem level experiments at Toolik Lake, Alaska, and at Abisko, Northern Sweden: generalizations and differences in ecosystem and plant type responses to global change. Global Change Biology 10: 105–123. https://doi.org/10.1046/j.1529-8817.2003.00719.x

Vinton M.A., Burke I.C. (1995). Interactions between individual plant species and soil nutrient status in shortgrass steppe. Ecology 76: 1116–1133. https://doi.org/10.2307/1940920

Väre H., Ohtonen R., Oksanen J. (1995). Effects of reindeer grazing on understorey vegetation in dry Pinus sylvestris forests. Journal of Vegetation Science 6: 523–530. http://dx.doi.org/10.2307/3236351

Walker M.D., Wahren C.H., Hollister R.D., Henry G.H.R., Ahlquist L.E., Alatalo J.M., Bret-Harte M.S., Calef M.P., Callaghan T.V., Carroll A.B., Epstein H.E., Jónsdóttir I.S., Klein J.A., Magnússon B., Molaug U, Oberbauer S.F., Rewan S.P., Robinson C.H., Shaver G.R., Suding K.N., Thompson C.C., Tolvanen A., Totland Ø., Turner P.L., Tweedie C.E., Webber P.J., Wookey P.A. (2006). Plant community responses to experimental warming across the tundra biome. PNAS 103: 1342-1346. http://dx.doi.org/10.1073/pnas.0503198103

Wilson S.D., Nilsson C. (2009). Arctic alpine vegetation change over 20 years. Global Change Biology 15:1676-1684. https://doi.org/10.1111/j.1365-2486.2009.01896.x

Wilmking M., Juday G.P., Barber V.A., Zald H.S. (2004). Recent climate warming forces contrasting growth responses of white spruce at treeline in Alaska through temperature thresholds. Global Change Biology 10: 1724–1736. https://doi.org/10.1111/j.1365-2486.2004.00826.x

Zellweger F., De Frenne P., Lenoir J., Vangansbeke P., Verheyen K., Bernhardt-Römermann M., Baeten L., Hédl R., Berki I., Brunet J., Van Calster H., Chudomelová M., Decocq G., Dirnböck T., Durak T., Heinken T., Jaroszewicz B., Kopecký M., Máliš F., Macek M., Malicki M., Naaf T., Nagel T.A., Ortmann-Ajkai A., Petřík P., Pielech R., Reczyńska K., Schmidt W., Standovár T., Świerkosz K.,Teleki B., Vild O., Wulf M., Coomes D. (2020). Forest microclimate dynamics drive plant responses to warming. Science 368: 772–775. https://doi.org/10.1126/science.aba6880